

MEMOIRS OF THE PEABODY MUSEUM OF NATURAL HISTORY
VOLUME IV, PART 1

Brachiopod Genera
of the
Suborders Orthoidea and Pentameroidea

BY

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All photographs of specimens figured on the plates were made by the author, with the assistance of Mr. Percy A. Morris. With the exception of Plate A, and Figure 24 of Plate 1, these photographs are entirely without retouching.

Page 57, column 1, line 14 from bottom, for *impunctate* read *punctate*.

Page 80, column 1, delete first two lines.

Page 81, column 2, line 7, for *Ozarkian* read *Canadian*.

Page 84, legend for Fig. 17, next to last line, for *left* read *right*.

Page 88, column 2, lines 14 and 15, delete *which is rather strongly convex*.

Page 109, column 2, lines 4 and 5, delete *We refer it doubtfully to our new genus Paurorthis*.

Page 141, table 14, *Aulacophoria* should be derived from *Schizophoria*, instead of from *Orthotichia*.



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BRACHIOPOD GENERA
OF THE
SUBORDERS ORTHOIDEA AND PENTAMEROIDEA



“The esthetic satisfaction to be derived from contemplating the mere variety of animal forms and from tracing the order that runs through all its diversity appeals to a very deep instinct in human nature.”

DAVID SHARP

“There is only one way of seeing things rightly, and that is seeing the whole of them.”

JOHN RUSKIN



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CONTENTS

| | Page |
|--|--------|
| INTRODUCTION | 1 |
| Division of work | 2 |
| Location of specimens | 3 |
| Technique | 3 |
| Species lists | 4 |
| Genetic lines | 4 |
| Acknowledgments | 4 |
| PART I. BRIEF DEFINITIONS OF BRACHIOPOD TERMS | 6 |
| PART II. PRINCIPLES OF MORPHOGENESIS OR EVOLUTION OF FORM | 12 |
| Need of taxonomy | 12 |
| Rise of brachiopod genera | 12 |
| The genus concept | 13 |
| Paleoecology | 16 |
| Homœomorphy | 16 |
| PART III. MORPHOLOGY OF THE ORTHOID SHELL | 18 |
| Morphology of the exterior | 18 |
| Orientation of the shell | 18 |
| Commissures | 19 |
| Convexity | 19 |
| Interareas | 20 |
| Deltidium | 21 |
| Modifications of the delthyrium (deltidium) | 21 |
| Function of the deltidium | 22 |
| Lateral plates | 23 |
| Modifications of the notothyrium (chilidium and chilidial plates) | 23 |
| Morphology of the ventral interior | 24 |
| Articulation | 24 |
| Teeth | 24 |
| Sockets | 25 |
| Dental plates | 25 |
| Spondylium | 26 |
| History of the term | 26 |
| Present views and definitions | 28 |
| Septa | 29 |
| Musculature | 30 |
| Pallial and genital markings | 32 |
| Pallial markings | 32 |
| Genital or ovarian markings | 33 |

| | |
|---|------|
| PART III. MORPHOLOGY OF THE ORTHOID SHELL— <i>Cont.</i> | Page |
| Morphology of the dorsal interior | 34 |
| Notothyrial platform | 34 |
| Denticles and sockets | 34 |
| Denticles | 34 |
| Sockets | 34 |
| Cardinalia | 34 |
| Cardinal process | 34 |
| Brachiophores or brachial apparatus | 37 |
| Cruralium and pseudocruralium | 39 |
| Septa | 39 |
| Musculature | 39 |
| Pallial markings | 40 |
| Microstructure of the shell | 41 |
| Exopunctæ | 42 |
| Endopunctæ | 42 |
| Value of punctation in taxonomy | 42 |
| Old-age characters | 42 |
| PART IV. THE GENERA OF THE SUBORDER ORTHOIDEA | 43 |
| Superfamily Orthacea | 43 |
| Family Nisusiidæ | 43 |
| <i>Nisusia</i> | 44 |
| <i>Jamesella</i> | 46 |
| Family Protorthidæ | 46 |
| <i>Protorthis</i> | 46 |
| <i>Loperia</i> | 47 |
| Family Billingsellidæ | 48 |
| <i>Billingsella</i> | 48 |
| Family Eoorthidæ | 50 |
| <i>Wimanella</i> | 50 |
| <i>Eoorthis</i> | 51 |
| <i>Otusia</i> | 52 |
| <i>Bohemiella</i> | 52 |
| <i>Oligomys</i> | 53 |
| Family Finkelburgiïdæ, nov. | 54 |
| <i>Orusia</i> | 54 |
| <i>Finkelburgia</i> | 55 |
| Family Plectorthidæ | 56 |
| Subfamily Plectorthinæ | 57 |
| <i>Plectorthis</i> | 57 |
| <i>Hebertella</i> | 59 |
| <i>Mimella</i> | 61 |
| <i>Schizophorella</i> | 62 |
| <i>Doleroides</i> | 63 |
| Subfamily Cyclocæliinæ | 64 |
| <i>Cyclocælia</i> | 64 |
| Subfamily Platystrophiinæ | 64 |
| <i>Platystrophia</i> | 64 |
| <i>Mcewanella</i> | 69 |

Superfamily Orthacea—*Cont.*Family Plectorthidæ—*Cont.*

| | |
|---------------------------------|------|
| | Page |
| Subfamily Orthostrophinae | 70 |
| <i>Orthostrophia</i> | 70 |
| <i>O. dartæ</i> , nov. | 71 |
| Family Skenidiidæ | 71 |
| <i>Skenidioides</i> | 71 |
| <i>S. billingsi</i> | 72 |
| <i>Skenidium</i> | 73 |
| Family Orthidæ | 73 |
| Subfamily Orthinæ | 75 |
| <i>Orthis</i> | 75 |
| <i>Cyrtonotella</i> | 77 |
| <i>Nicolella</i> | 77 |
| <i>Glossorthis</i> | 78 |
| <i>Paurorthis</i> | 79 |
| <i>Archæorthis</i> | 80 |
| Subfamily Productorthinæ | 81 |
| <i>Panderina</i> | 81 |
| <i>Productorthis</i> | 82 |
| Subfamily Angusticardiniinæ | 84 |
| <i>Angusticardinia</i> | 84 |
| Subfamily Taffinæ | 85 |
| <i>Taffia</i> | 85 |
| <i>Eostrophomena</i> | 85 |
| Subfamily Hesperorthinæ | 85 |
| <i>Hesperorthis</i> | 87 |
| <i>Schizorammina</i> | 88 |
| <i>S. gotlandica</i> , nov. | 88 |
| <i>Dolerorthis</i> | 89 |
| Subfamily Glyptorthinæ | 89 |
| <i>Glyptorthis</i> | 91 |
| <i>Eridorthis</i> | 92 |
| <i>Ptychopleurella</i> | 93 |
| <i>P. matapedia</i> , nov. | 93 |
| Family Dinorthidæ | 93 |
| <i>Dinorthis</i> | 95 |
| <i>Dinorthis s. s.</i> | 95 |
| <i>Plæsiomys</i> | 95 |
| <i>Retrorsirostra</i> | 95 |
| <i>Pionorthis</i> | 96 |
| <i>Marionella</i> | 97 |
| <i>Valcourea</i> | 98 |
| <i>V. magna</i> , nov. | 98 |
| <i>Multicostella</i> | 99 |
| <i>Austinella</i> | 100 |
| <i>Palæostrophomena</i> | 100 |
| <i>Planidorsa</i> | 101 |
| <i>P. bella</i> | 101 |
| <i>P. crassicostella</i> , nov. | 101 |
| Family Porambonitidæ | 101 |
| <i>Porambonites</i> | 102 |
| <i>Noetlingia</i> | 105 |
| Family Lycophoriidæ | 105 |
| <i>Lycophoria</i> | 105 |

PART IV. THE GENERA OF THE SUBORDER ORTHOIDEA—*Cont.*

| | Page |
|---|------|
| Superfamily Clitambonacea | 107 |
| Family Deltatretidæ | 107 |
| <i>Deltatreta</i> | 108 |
| <i>Pomatotrema</i> Ulrich and Cooper, nov. | 109 |
| <i>P. muralis</i> Ulrich and Cooper, nov. | 109 |
| <i>Polytæchia</i> | 110 |
| Family Clitambonitidæ | 110 |
| Subfamily Plectellinæ | 112 |
| <i>Plectella</i> | 112 |
| <i>Ingria</i> | 112 |
| Subfamily Clitambonitinæ | 113 |
| <i>Clitambonites</i> | 113 |
| <i>Vellamo</i> | 114 |
| <i>Clinambon</i> , nov. | 115 |
| <i>Estlandia</i> | 115 |
| <i>Hemipronites</i> | 115 |
| <i>Pahlenella</i> | 117 |
| <i>Apomatella</i> | 117 |
| Subfamily Gonambonitinæ | 118 |
| <i>Gonambonites</i> | 118 |
| Superfamily Dalmanellacea | 119 |
| Family Dalmanellidæ | 119 |
| <i>Dalmanella</i> | 120 |
| <i>Cariniferella</i> | 122 |
| <i>Aulacella</i> | 122 |
| <i>Proschizophoria</i> | 123 |
| <i>Levenea</i> | 123 |
| <i>Heterorthina</i> | 124 |
| Family Wattsellidæ | 124 |
| <i>Wattsella</i> | 125 |
| <i>Resserella</i> | 126 |
| <i>Horderleyella</i> | 127 |
| <i>Mendacella</i> | 127 |
| <i>Idiorthis</i> | 128 |
| <i>Parmorthis</i> | 128 |
| <i>P. crassicostata</i> , nov. | 129 |
| <i>Fascicostella</i> | 129 |
| Family Bilobitidæ | 130 |
| <i>Bilobites</i> | 130 |
| Family Mystrophoridæ | 131 |
| <i>Mystrophora</i> | 131 |
| <i>Kayserella</i> | 132 |
| Family Rhipidomellidæ | 133 |
| <i>Rhipidomella</i> | 133 |
| <i>Perditocardinia</i> | 135 |
| <i>Platyorthis</i> | 135 |
| <i>Thiemella</i> | 136 |
| Family Heterorthidæ | 136 |
| Subfamily Heterorthinæ | 137 |
| <i>Heterorthis</i> | 137 |
| Subfamily Harknessellinæ | 138 |
| <i>Harknessella</i> | 138 |
| <i>Reuschella</i> | 139 |
| <i>Smeathenella</i> | 139 |

| | |
|--|------|
| Superfamily Dalmanellacea— <i>Cont.</i> | Page |
| Family Schizophoriidæ | 139 |
| Subfamily Schizophoriinæ | 140 |
| <i>Pionodema</i> | 141 |
| <i>Schizophoria</i> | 143 |
| <i>Orthotichia</i> | 144 |
| <i>Aulacophoria</i> | 145 |
| Subfamily Enteletinæ | 145 |
| <i>Enteletes</i> | 146 |
| <i>Parenteletes</i> | 147 |
| <i>Enteletina</i> | 148 |
| <i>Enteletella</i> | 148 |
| <i>Enteletoides</i> | 148 |
| Subfamily Isorthinæ | 149 |
| <i>Isorthis</i> | 149 |
| Family Linoporellidæ | 150 |
| <i>Linoporella</i> | 150 |
| <i>Orthotropia</i> | 152 |
| Family Tropicodoleptidæ, nov. | 152 |
| <i>Tropicodoleptus</i> | 152 |
| PART V. THE GENERA OF THE SUBORDER PENTAMEROIDEA | 154 |
| Superfamily Syntrophicea | 154 |
| Family Clarkellidæ | 155 |
| <i>Syntrophoides</i> | 155 |
| <i>Syntrophina</i> | 155 |
| <i>Clarkella</i> | 156 |
| <i>Yangtzeella</i> | 157 |
| Family Syntrophiidæ | 158 |
| <i>Syntrophia</i> | 158 |
| <i>Swantonina</i> | 159 |
| Family Huenellidæ | 159 |
| <i>Huenella</i> | 159 |
| <i>Huenellina</i> | 160 |
| Superfamily Pentameracea | 161 |
| Technique | 162 |
| Morphology of the Pentameracea | 162 |
| Exterior | 162 |
| Ventricosity | 162 |
| Ornamentation | 162 |
| Interareas | 163 |
| Ventral interior | 163 |
| Delthyrium | 163 |
| Deltidial cover | 163 |
| Deltidial plates | 163 |
| Spondylium | 164 |
| Dorsal interior | 164 |
| Septa | 164 |
| Musculature | 164 |
| Cardinalia | 164 |

PART V. THE GENERA OF THE SUBORDER PENTAMEROIDEA—*Cont.*Superfamily Pentameracea—*Cont.*

| | Page |
|--|------|
| Generic and evolutionary trends | 165 |
| Loss of interareas and development of a planarea | 165 |
| Rostration | 165 |
| Reversion of normal convexity | 165 |
| Trilobation | 165 |
| Ornamentation | 165 |
| Loss of the ventral septum | 166 |
| Development of a cruralium | 166 |
| Parallel trends | 166 |
| Summary | 166 |
| Family Camerellidæ | 166 |
| <i>Camerella</i> | 167 |
| <i>Branconia</i> | 168 |
| <i>Parastrophinella</i> | 169 |
| <i>Anastrophia</i> | 169 |
| <i>Metacamerella</i> | 170 |
| Family Pentameridæ | 170 |
| Subfamily Gypidulinæ | 171 |
| <i>Clorinda</i> | 171 |
| <i>Barrandella</i> | 173 |
| <i>Gypidula</i> | 173 |
| <i>Sieberella</i> | 175 |
| <i>Pentamerella</i> | 176 |
| <i>Zdimir</i> | 177 |
| Subfamily Pentamerinæ | 177 |
| Læves | 177 |
| <i>Pentamerus</i> | 177 |
| <i>Pentameroides</i> | 179 |
| <i>Lissocœlina</i> | 179 |
| <i>Capelliniella</i> | 179 |
| <i>Holorhynchus</i> | 180 |
| <i>Harpidium</i> | 180 |
| Costatæ | 180 |
| <i>Rhipidium</i> | 180 |
| <i>Conchidium</i> | 181 |
| <i>Brooksina</i> | 183 |
| <i>Cymbidium</i> | 183 |
| <i>Platymereella</i> | 184 |
| <i>Virgiana</i> | 185 |
| Family Stricklandidæ | 186 |
| <i>Stricklandia</i> | 187 |

| | |
|-------------------------------------|-----|
| APPENDIX | 189 |
| ? Superfamily Rhynchonellacea | 189 |
| <i>Rhynchocamara</i> | 189 |
| <i>Liocœlia</i> | 189 |
| INDEX | 257 |

INTRODUCTION

Brachiopods have interested the senior author since the days of his early youth, and by 1886, while assistant to E. O. Ulrich in Cincinnati, he had a private collection of them so large and well arranged that it led James Hall to transport collection and collector to Albany to assist him in the work then in preparation, "An Introduction to the Study of the Genera of Palæozoic Brachiopoda" (1892-1894). This recognition stimulated Schuchert all the more to add to his collection, which he has continued to do ever since, with the exception of the twelve years spent as curator at the United States National Museum, where each official is expected to devote his entire attention to the care and increase of the Government collections. The first great addition was made in 1884, when the brachiopods gathered by E. O. Ulrich were obtained, and later through purchase came the Ernst H. Vaupel and other smaller collections from the Ohio Valley. At Albany was purchased the John M. Clarke collection of Middle Devonian fossils. All the non-brachiopod material in these purchases was exchanged with the dealers Braun of New York and Krantz of Bonn, Germany, for European brachiopods, with the permission of the authorities of the National Museum.

Upon taking up the chair of paleontology at Yale University in 1904, the stimulus to acquire more brachiopods was renewed. The Marshall collection of English Jurassic Telotremata was purchased in 1909 through S. S. Buckman, who relabeled the material carefully, especially with regard to stratigraphic horizons; and later the private collection of Fred Braun of New York, also rich in European species, which that dealer had long been accumulating. Largest of all the acquisitions, however, enriching the Schuchert Collection by many thousands of fine Paleozoic specimens, was the private collection of D. K. Greger, most of which that devoted gatherer of brachiopods had assembled, during a long life, from the Mississippi Valley and the Southwest. With this material came an extensive library of brachiopod literature, which, together with that already in the Peabody Museum, forms the still growing Schuchert-Greger Brachiopod Library of that institution.

From these statements it is apparent that the authors of the present work had access to one of the largest brachiopod collections known. For Cambrian material, without which no genetic study of brachiopod genera can have a secure foundation, we had the privilege of access to the most extensive collections known from rocks of this period, made by Charles D. Walcott and forming one of the great treasures of the United States National Museum.

At Washington the curatorial duties of the senior author made it impossible to take up any protracted paleontological studies, due to the rapid growth and constant need for rearrangement of the National Museum collections; but he did bring to final form a card catalogue of brachiopod genera and species which he had begun at Cincinnati, and which appeared in print in 1897 as Bulletin 87 of the United States Geological Survey. With his transfer to Yale, the hope of working up his collections was reborn, but here again, due to university and administrative duties, it soon became evident that if anything worth while was to be done, it must come through a colleague who could devote his entire time to a restudy of the genera. For many years, however, neither adequate scholarships nor museum appointments could be found, but, with the hope still in mind, the senior author laid aside savings out of his salary and out of royalties accruing from the sale of his textbooks. Finally, in 1925, there came to Yale a post-graduate student, the junior author, who soon showed that he possessed the necessary qualifications and inclination to undertake the work.

In the beginning privat-dozent and professor emeritus built "castles in Spain," contemplating a revision of all the brachiopod genera, but caution led them to start with the most primitive of the articulate forms, the orthoids. What an undertaking the original intention would have been is seen in Schuchert and LeVene's "Generum et Genotyporum Index et Bibliographia" of 1929, which lists about 700 valid genera, of which 456 are Paleozoic, 177 Mesozoic, and 74 Cenozoic-Recent.

The senior author had also become suspicious that all was not correct in regard to the origin of the Telotremata as held by Beecher (1891) and Schuchert (1897), and in regard to the supposed primordial significance of the deltidium in the Protremata, and of what had been called the pro-

deltidium. Yatsu (1902, 1905) had shown that there was no "third plate" in embryonic shells and that therefore the formation of a deltidium could not have started in this way. This again raised the question: Of what significance in classification is the deltidium? In the meantime Walcott's classic "Cambrian Brachiopoda" (1912) had shown that among these early forms there were no Telotremata (*Swantonina* is not of this order, as was then believed), and that the few forms regarded as Strophomenacea were probably orthoids. After we had started our studies came a penetrating little book entitled "Brachiopod Morphology and Genera (Recent and Tertiary)" by that clear-thinking author, the late J. Allan Thomson, which made still more apparent the necessity for a revision of the Paleozoic articulate brachiopods.

As is well known, studies along fundamental lines take much more time than generic revision, and as time wore on our Spanish castles showed signs of shrinkage, and we had to limit ourselves to Paleozoic genera. Along this line we were proceeding nicely when the call came for the junior author to take up a position as assistant curator in the United States National Museum, and we had to write "finis" to our work with only one-half of the Protremata done and the Telotremata not more than started. However, we have an abundance of results, showing that the Orthacea, or rather the greater division that we are calling Orthoidea, contains the primary stock from which all the articulate brachiopods have arisen! This means not only that the Pentameracea and the Strophomenacea have evolved out of the Orthacea, but that the order Telotremata had its origin here as well. We have indicated these beginnings and regret that conditions prevent our proving the genetic lines. However, a need once pointed out will soon be taken up by others, though we hope that it may be our privilege to follow these leads further, either through independent work by the junior author, or through studies at Yale by another budding paleontologist.

Table of the groupings discussed in the following pages

| | Total | New | Old |
|---|-------|-----|-----|
| Orders | 2 | | 2 |
| Suborders (Orthoidea and Pentameroidea) | 2 | 2 | |
| Superfamilies | 5 | 2 | 3 |
| Families | 28 | 15 | 13 |
| Subfamilies | 20 | 11 | 9 |
| Genera and subgenera | 135 | 35 | 100 |

| | | | Genera- Subgenera | Genera known in 1929 |
|---------------|-------------|-------------|----------------------|----------------------------|
| Superfamilies | Families | Subfamilies | | |
| Orthacea | 11 (6 new) | 10 (7 new) | 103 { 53 (15 new) | 52 |
| Clitambonacea | 2 (1 ") | 3 (2 ") | { 13 (4 ") | |
| Dalmanellacea | 9 (6 ") | 5 (2 ") | { 37 (10 ") | |
| Syntrophiacea | 3 (2 ") | 0 | 32 { 8 (2 ") | 26 |
| Pentameracea | 3 | 2 | { 24 (4 ") | |
| | 28 (15 new) | 20 (11 new) | 135 (35 new) | 78 |

DIVISION OF WORK.—The senior author, as intimated above, made it financially possible for his co-laborer to devote himself wholly for two years to this study of the Brachiopoda, and also turned over to him for use his collection and library. He then sketched out the plan of work and passed on the brachiopod lore accumulated during a lifetime, and stimulated by association with E. O. Ulrich, James Hall, John M. Clarke, and Charles E. Beecher. The bulk of the detailed results were thus attained by the junior author, under the guidance of the senior author and of our colleague, Professor Carl O. Dunbar, who was at the time himself engaged in a revision of the Pennsylvanian brachiopods of the Nebraska region.

The study so carried on has led to departures from the older lore as radical as were those of Hall and Clarke between the years 1890 and 1895. These results, we are fully aware, will in turn have to face the test of new facts brought to light by later workers. Nevertheless we are content to

send them forth as a contribution to the evolutionary history of the brachiopods—a study the importance of which was well seen by Charles Darwin when he unavailingly appealed to the leading specialist of his time, Thomas Davidson, to take up the brachiopods from the standpoint of descent through evolution.

LOCATION OF SPECIMENS.—As indicated above, this memoir is based mainly on material in the Schuchert Brachiopod Collection in the Peabody Museum of Yale University. Specimens from this collection have the letter S preceding the catalogue number (e. g., S 12). Specimens from other collections in the Peabody Museum have the letters Y.P.M. following the catalogue number (e. g., 120 Y.P.M.).

TECHNIQUE.—In any critical revision of brachiopod genera it is paramount to know every detail of the shells with which one is dealing. It is not difficult to find brachiopods in the field showing the exterior, as free specimens or as molds in the rock; it is far more difficult to find free valves with the interiors cleaned by nature, or as sharp molds. In the Schuchert Collection by far the majority of the specimens are free individuals showing the exterior in good detail. This is a consequence of the collection's being a composite one, built up of choice material brought together by many skilled collectors. To be sure, there are great numbers of interiors in the collection, but not of every genus. Accordingly, it became necessary to prepare interiors for a large number of the genera that we studied. We were able, by various methods, to obtain the essential details of the internal anatomy of every genus with which we worked. There is really no reason why, given plenty of material, the interior of every genus of brachiopods should not be known.

The following methods were used in securing the internal anatomy of the brachiopod shell:

(1) etching, (2) cleaning with needles, (3) burning, and (4) serial sectioning (Zugmayer process).

(1) When specimens of dissociated valves are filled with shale or clay, the internal surface may be obtained by placing on the specimen lumps of potash and allowing the chemical to deliquesce. The potash then attacks the shale and loosens it. This method is not always satisfactory, however, because the potash usually attacks the substance of the shell, producing a white efflorescence which can be got rid of only by the use of dilute acid. This means the loss of some details of the surface, and is undesirable when other methods can be pursued.

When shells are silicified they can as a rule be freed from the limestone by dissolving the matrix in dilute hydrochloric acid. Care must be taken, however, to use exceedingly dilute acid, otherwise the shell itself may be attacked or be disrupted by violent ebullition of gas. It is not usual to find shells properly silicified, but when one does, they show the internal characters exceedingly well.

(2) More laborious, but more satisfactory by far, than the use of potash is the careful manipulation of a needle accompanied by a dentists' drill. With this combination the interior of most brachiopods can be obtained. We found it most satisfactory to cement the specimen in plaster of paris and then excavate the interior with a needle, carrying on all the manipulations under a binocular microscope. This method requires time and patience, but when one has prepared successfully the interior of a rare shell, he is amply repaid for the expenditure of one-half to a day's time. In some instances we took specimens in which both valves were in contact and secured the interior of one or the other valve, depending on which we wanted. If the ventral interior was desired, the dorsal valve was ground off, the remaining one cemented in plaster and excavated by the use of a needle. The majority of the interiors figured in this memoir were prepared by the use of a needle.

(3) John M. Clarke and S. S. Buckman were the pioneers in the use of the method of burning or calcining the shells of brachiopods. This method was used by the latter to good advantage in his splendid treatise on the Burma brachiopods. Buckman heated the shells to redness and dropped them into water, the shell spalling off in the process. We found, however, that the dropping of the shells into water was disastrous to the specimen in certain types of matrices. It is more satisfactory to heat the shells in air to redness, and, after cooling, to scrape the shell off with a sharp needle. The process of heating softens the shell and allows it to be removed rather easily. Natural casts of interiors made by this method, and internal molds in general, have their limitations; they are excellent for details of the muscle-scars, but it is usually difficult to get sharp impressions of the cardinalia, which are best seen in free valves.

(4) We used serial sectioning as a last resort, since this method usually means the total loss of the specimen. We developed a method, however, in the study of the pentameroids, by which we were able to save a thin section of the shell as a result of serial sectioning. This method is described in the chapter on the Pentameroidea, as we were not obliged to use it to any great extent in the study of the Orthoidea; it is of great aid among the rhynchonellids, spiriferids, and terebratulids, where the interiors are of hard cemented rock.

SPECIES LISTS.—Throughout our paper we have listed under each genus the known species which we believe have the structure of the genus as exhibited by the genotype. In some instances our lists are complete, in others they are quite incomplete. Among the Cambrian brachiopods, for example, there are a goodly number of species left unplaced because there was no hint of the internal structure in the specimens available to us, and we would not place any of the species unless we could feel reasonably sure that our reference was correct. Our lists are incomplete also because we made no systematic attempt to track down in the literature all of the species of the Orthoidea and Pentameroidea. Although this might have been desirable, we would doubtless have had to leave a large number of these unplaced, too, because of lack of material or inadequate descriptions and figures, particularly in the older literature. Therefore we placed only the species that came under our direct observation. Some familiar species we left out because we could not establish any substantial generic reference for them. An example is "*Orthis*" *eminens*, which has been placed by various writers in *Rhipidomella* or *Dalmanella*, but belongs to neither. It appears to be closest to *Idiorthis* in internal structure but varies too notably to be placed there. It appeared to us better to admit honestly that we did not know what to do in certain instances. After us there will be many readjustments and many new genera will ultimately gather home the flocks we have left to wander.

GENETIC LINES.—A note regarding the diagrams of generic evolution which appear in the discussion of the families is necessary. These diagrams are designed to be suggestive and not final. There is probably only one family described by us whose evolution has been fairly well established, and that is the Schizophoriidæ. But there are difficulties even here: we do not know the Middle Ordovician (Chazy) progenitor of the group, nor do we know definitely the origin of *Enteleles*, whether directly from *Schizophoria* or indirectly from that genus through *Orthotichia*. Our family Plectorthidæ can be traced to *Finkelburgia* and possibly to *Orusia*, but the antecedents beyond those genera we can not find. It must be borne in mind that the late Cambrian and early Ordovician brachiopods are virtually unknown and that here occur the genera that bridge the genetic gaps between the Middle Ordovician (Chazy) and the Upper Cambrian. It might be suggested, too, that the Chazy brachiopods are none too well known. Accordingly we find ourselves without sure footings among the primitive brachiopods upon which to build our evolutionary structure. It is therefore unwise at this time to link the known Cambrian forms with those of later time.

We might again cite an example. It has been maintained by some writers that the genus *Billingsella* gave rise to the Strophomenacea, and *Eostrophomena*, a Lower Ordovician shell, has been indicated as the forerunner of that great division. We now see that *Eostrophomena* is an orthid. Furthermore, genuine Strophomenacea are not known till Middle Ordovician (Chazy) time.

At most, what we are trying to do is to show that the indicated evolution is *structurally possible*, but we can not say that our scheme represents the actual course of evolution. Our genera are, therefore, rather iceloplasmic types¹ having the structure capable of producing the evolution indicated, but this does not necessarily define the actual course of brachiopod genesis.

ACKNOWLEDGMENTS.—During the progress of our work it has often been necessary to call on specialists and others in order to see more material and to obtain advice along various lines. Everywhere we turned for assistance we have been aided very cheerfully. Miss Helen M. Muir-Wood of the British Museum kindly loaned us an excellent series of specimens of the genus *Schizophorella*; Doctor A. H. Westergaard of the Geological Survey of Sweden, at Stockholm, sent us for study specimens of "*Dalmanella*" *testudinaria* which enabled us to make the astonishing discovery that the chosen type of *Dalmanella* was different generically from all other American species referred to this genus except one. Doctor Westergaard also loaned us an exquisite series of *Orthis punctata* showing

¹ Kirk, Amer. Jour. Sci. (5), vol. 18, 1929, p. 345.

the interior from youthful to old-age stages, which made it possible for us to understand the development of the pseudospondylium. Doctor Chester A. Reeds of the American Museum of Natural History sent us the Conrad types of *Pionodema*, and through Doctor H. W. McGerrigle of Dartmouth College we were able to study a good series of *Clarkella*, *Syntrophina*, and *Finkelburgia* from the Phillipsburg region of Quebec. Doctor E. M. Kindle of the Geological Survey of Canada permitted the study of Billings' types of *Orthis electra*, now the types of our genus *Archæorthis*. Professor Paul H. Dunn of Miami University helped us with material of *Eridorthis*. Through Professor Percy E. Raymond, the Museum of Comparative Zoölogy of Harvard College loaned us a collection of European brachiopods particularly rich in representatives from the vicinity of Leningrad. Doctor B. B. Bancroft of the Sedgwick Museum, Cambridge, England, and Doctor A. Öpik of the University of Tartu, Estonia, sent us very perfect and interesting specimens of their new genera which are not well known in this country, and many of these specimens have been figured by us.

Through the courtesy of Doctors R. S. Bassler and C. E. Resser of the United States National Museum the junior author was allowed to study the incomparable collection of Cambrian brachiopods there preserved. Doctor E. O. Ulrich of the United States Geological Survey and the National Museum loaned us some of his choice specimens of the very rare genera *Mcewanella*, *Deltatrete*, and *Finkelburgia*. Through Miss Winifred Goldring of the New York State Museum we had access to specimens of the strange genus *Australina*, which we were able to determine definitely as a representative of some division of brachiopods other than the Dalmanellidæ where the senior author had previously placed it.

To Miss Clara Mae LeVene we are deeply grateful for her patient and exhaustive labors on our manuscript, to Mr. Percy A. Morris for assistance in the preparation of the photographs and figures, and to Doctor J. B. Knight, research associate in the Peabody Museum, for the generous loan of instruments used in preparing fossils.

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PART I. BRIEF DEFINITIONS OF BRACHIOPOD TERMS¹

ADDUCTOR MUSCLES (pl. A, figs. 4, 13).—The muscles that close the shell. In the Protremata and Telotremata these muscles are inserted in the ventral valve, one on either side of the central axis, between the diductors (*q. v.*). In passing to the dorsal valve they divide into four, and produce in that shell the two pairs of principal scars known as the anterior and posterior **ADDUCTOR SCARS**.

ADJUSTOR MUSCLES.—Included in the pedicle muscles, *q. v.*

ADVENTITIOUS DEPOSIT (pl. A, figs. 7, 10).—Extra fibrous shell substance deposited by the mantle on the inside of the shell, filling up cavities and irregularities of the surface. By deposition of such adventitious shell in the umbonal cavities, the dental plates may be obliterated.

ANACLINE.—See Pt. III, **INTERAREAS**, and t. fig. 1.

ANTERIOR.—That portion of the shell in front of the hinge region, away from the beaks.

APICAL PLATE (pl. 23, fig. 9).—A small flat structure situated in the apex of the delthyrium and flush with the interareas. To the under side of it probably was attached the pedicle. This plate is not a relict of the deltidium.

APSACLINE.—See Pt. III, **INTERAREAS**, and t. fig. 1.

AREA.—See **INTERAREA**.

ARTICULATION.—The locking together of the two valves, effected in the main by the teeth of the ventral valve moving in sockets in the dorsal valve, but further assisted by the brachial parts (brachiophores) articulating with the ventral valve, at least in orthoid genera.

BRACHIAL VALVE.—See **DORSAL VALVE**.

BRACHIDIA.—Calcareous brachial supports in the spire- and loop-bearing brachiopods.

BRACHIOPHORES (pl. A, fig. 7; pl. 4, fig. 29).—Plates that bound the notothyrial cavity (*q. v.*) in the orthids. More commonly known as socket-plates or brachial apparatus. In a few genera, **BRACHIOPHORE PROCESSES** are seen to extend from the distal extremity of the brachiophores, and to them were undoubtedly attached the brachia. The brachiophores may be the homologues of the crural bases of the rhynchonellids, but in any event are more primitive than the latter.

BRACHIOPHORE SUPPORTS (pl. A, fig. 14; pl. 11, fig. 26).—Plates attached to the dorsal face of the brachiophore, and used to strengthen the latter. Known in *Hebertella* and *Schizophoria*.

CAMERA.—See **CELLA**.

CARDINAL ANGLES.—Angles formed at each of the extremities of the hinge between it and the forward extension of the shell.

CARDINAL AREA.—See **INTERAREA** and **PALINTROPE**.

CARDINAL PROCESS (pl. A, figs. 4, 6, 10).—A median unpaired process, lying immediately on the inner side of the dorsal umbo, and serving for the attachment of the diductor muscles.

CARDINALIA.—Processes near the posterior or cardinal margin in the interior of the dorsal valve, connected with articulation, muscle attachment, and attachment of brachial supports. (After Thomson 1927.)

CATACLINE.—See Pt. III, **INTERAREAS**, and t. fig. 1.

CELLA (pl. 24, figs. 21, 26).—A small, inverted, V-shaped chamber beneath or ventrad to the ventral median septum of *Parenteleles*. A similar structure occurs in *Dayia*, *Cyclospira*, and *Camarium* (*Merista*).

CHILIDIAL PLATES (pl. 16, fig. 22).—Discrete plates, one on either side of the notothyrium, and partially closing it.

¹ For further discussion of many of these terms, see Part III, Morphology.

CHILIDIUM (pl. A, figs. 4, 6, 7).—The covering of the notothyrium, the dorsal equivalent of the ventral deltidium.

COMMISSURE.—The boundary line between the anterior and lateral margins of the valves. It may lie in a single plane or be flexed to a greater or less degree. See **PLANE OF COMMISSURE** and **RECTIMARGINATE**.

CONVEXITY.—In describing the convexity of a brachiopod, the dorsal valve is named first; this is for the sake of making comparisons always in the same direction, namely, from dorsal above to ventral below. For example, *Valcourea deflecta* would be spoken of as convexo-concave and *Orthis callactis* would be termed concavo-convex. See **RESUPINATE**.

COSTA (**COSTÆ**).—A coarse radial rib on the external surface. When a species has costæ that are simple and distant it may be called **PAUCICOSTATE**; when the costæ are numerous and increase by bifurcation or implantation it is **MULTICOSTATE**; and when they are bundled into fascicles the term **FASCICOSTATE** may be employed. Costæ may be angular, subangular, or rounded.

COSTELLA (**COSTELLÆ**).—Fine external ribs such as those of *Dalmanella*. The same prefixes may be used in connection with this term as with costæ. Extremely fine radial lines, such as those on the costæ of *Orthis s. s.*, may be termed **PARVICOSTELLÆ**.

CRURA (sing. **CRUS**).—Processes in the dorsal valve of the Telotremata to which are attached the fleshy brachia or the brachidia. See **BRACHIOPHORE**.

CRURAL FOSSETTE (pl. A, fig. 15).—An excavation on the inner face of the tooth of the ventral valve which receives the postero-ventral edge of the dorsal brachioophore in the articulation of the shell.

CRURAL PLATE.—A general term commonly applied to the brachial processes of the orthids, strophomenids, and rhynchonellids, without regard to detailed structure, function, or homologies.

CRURALIUM (pl. 18, fig. 17; pl. 25, fig. 24).—The dorsal equivalent of the ventral spondylium (*q. v.*). When the brachial lamellæ unite with a median septum, the whole structure is called a **CRURALIUM SIMPLEX**; when the brachial plates remain discrete, do not have the muscle attachments, and do not unite with a median septum (as in *Porambonites*), the structure is known as a **DISCRETE CRURALIUM**; and when there is no median septum, it is called a **SESSILE CRURALIUM**.

DELTARIUM.—See **DELTIDIAL PLATES**.

DELTHYRIAL CAVITY (pl. A, fig. 15).—The ventral umbonal cavity bounded by the dental plates.

DELTHYRIUM.—The triangular aperture which transects the ventral interarea medially, and through some portion of which the pedicle passes. It has also been termed the **FISSURE**. The delthyrium may or may not be closed by a deltidium or deltidial plates. Its equivalent in the dorsal valve is the notothyrium (*q. v.*).

DELTIDIAL PLATES.—In Telotremata, two plates growing medially from the walls of the delthyrium after neanic growth. These often unite medially, closing the delthyrium more or less completely. When united, they make a **DELTARIUM** = symphytium of Buckman, pseudodeltidium of Schuchert (not Bronn or Walcott). In Protremata, similar plates are at times developed and these are called **LATERAL PLATES** (*q. v.*).

DELTIDIUM (pl. A, fig. 2).—An independent, more or less strongly arched plate in the ventral palintrope or cardinal area in many Protremata, growing from the apex toward the hinge-line and partly or completely covering the delthyrium. It is always delimited from the interarea by grooves. It is characteristic of primitive shells, and is formed by a flap of the ventral mantle.

DENTAL PLATES or **DENTAL LAMELLÆ** (pl. A, fig. 5).—Vertical or nearly vertical plates associated with the teeth of the ventral valve, usually uniting the palintrope to the floor of the valve, and bounding the delthyrial cavity. They are separated from the walls of the shell by the umbonal cavities. When the latter have been filled by adventitious shell, the dental plates become **OBSOLETE**. A special type of dental plates seen in *Hesperorthis*, etc., is called **RECEDING DENTAL PLATES**. These are ridges along the ventral surface of the palintrope, which finally reach the inner surface of the valve at the posterior of the shell only.

DENTAL SOCKETS.—Excavations in the dorsal cardinal margin in which the teeth of the ventral valve articulate. The inner wall of the socket is bounded by the brachiophore in orthids. **ACCESSORY DENTAL SOCKETS**, see **SOCKETS**.

DENTICLES (pl. 10, fig. 21).—Small processes on the posterior surface of the dorsal socket which are inserted into the accessory sockets in the ventral teeth.

DIDUCTOR MUSCLES (pl. A, fig. 13).—The muscles that open the valves. In the Protremata and Telotremata the principal pair has the larger end attached to the ventral valve near the anterior edge of the visceral area, while the other end has its insertion on the posterior portion of the cardinal process. There is another pair of small accessory diductor muscles, but scars of these are seldom shown in fossil shells. When present they are situated just behind the adductor impressions.

DORSAL DIRECTION.—Toward the dorsal valve, at right angles to the plane of the commissure.

DORSAL MEDIAN RIDGE (pl. A, figs. 7, 8).—A low axial thickening on the dorsal interior of most orthids and rhynchonellids. See **MEDIAN SEPTUM**.

DORSAL VALVE.—Usually the smaller valve, and the one to which the brachia are always attached. **BRACHIAL** and **SOCKET VALVE** are other terms less often used.

In this work we shall stand by the biological usage of naming the two valves ventral and dorsal, a position that is fortified by the work of Conklin,² which showed, from the orientation of the embryo, that the valves are truly ventral and dorsal, although in nature the adult shells usually have the ventral valve uppermost.

DUPLEX SPONDYLUM.—See **SPONDYLUM SIMPLEX**.

ENDOPUNCTÆ.—See **PUNCTÆ**.

EUSEPTUM (pl. A, fig. 5).—A ventral median ridge formed by the inner shell layers rising into a septum that usually makes the seat of attachment for the adductor muscles.

EXOPUNCTÆ.—See **PUNCTÆ**.

FASCICOSTATE.—See **COSTÆ**.

FASCICOSTELLATE.—See **COSTELLÆ**.

FILÆ.—Fine elevated concentric lines.

FOLD (pl. 24, figs. 5, 19).—A broad median external undulation or plica that may be situated on either the dorsal or ventral valve, hence dorsal or ventral fold. It is more commonly on the dorsal valve. Its counterpart is **SULCUS**, *q. v.*

FORAMEN.—See **PEDICLE FORAMEN**.

FOSSETTE.—See **CRURAL FOSSETTE**.

FULCRAL PLATES (pl. A, fig. 14).—Small concave plates attached to the outside wall of the brachiophore support or brachiophore and the inner wall of the shell. These serve to define the sockets and strengthen the brachiophore supports.

GENITAL MARKINGS (pl. 12, figs. 20, 24).—Radial markings, ridges, or pits within the posterior portion of the visceral space, indicating the position and extent of the genitalia, and used for the attachment of muscles which fix the ovarian bodies. Best seen on the ventral shell.

GERONTIC.—Signifying old age.

HINGE-LINE.—The line along which articulation takes place.

HYPERCLINE.—See **Pt. III**, **INTERAREAS**, and t. fig. 1.

INTERAREA.—The posterior plane or curved surface lying between the apex and the line of valve junction. Formerly called cardinal area.

LATERAL AREAS.—The parts of the valves on either side of the median axis or on either side of the fold and sulcus.

² Conklin, E. G., The embryology of a brachiopod, *Terebratulina septentrionalis* Couthouy. Proc. Amer. Philos. Soc., vol. 41, 1902, pp. 41-76.

LATERAL PLATES (pl. A, fig. 11).—External marginal plates restricting the delthyrium and seen only in certain orthids and pentamerids. These discrete plates appear to be formed in exactly the same manner as deltidial plates, *q. v.*

LATERAL SEPTA.—See **MEDIAN SEPTUM**.

MEDIAN RIDGE.—See **DORSAL MEDIAN RIDGE**, and **MEDIAN SEPTUM**.

MEDIAN SEPTUM (pl. A, figs. 5, 9).—A longitudinal vertical plate between the ventral muscles. **LATERAL SEPTA** are rarely developed between the muscles of the same valve, but are more often present when spondylia are developed.

MULTICOSTATE.—See **COSTÆ**.

MUSCLE IMPRESSIONS.—Marks of muscle attachment on the shell, further subdivided as follows: **MUSCLE-SCAR**, a more or less well defined area representing the final or last muscle attachment. **MUSCLE-TRACK**, the path due to the forward migration of the muscles during growth.

MYOPHORE (pl. 9, figs. 3, 20; pl. 17, figs. 31, 32).—The rugose surface of muscle attachment on the cardinal process. See **SHAFT**.

NEANIC.—Signifying youth, or the stage in which specific characters begin to develop.

NEPIONIC.—Designating the smooth-shell stage succeeding the protegulum.

NOTOTHYRIAL PLATFORM (pl. 1, fig. 23).—The thickened shell matter in the umbonal interior of the dorsal valve between the brachiphore plates. It is the seat of diductor muscle attachment in primitive brachiopods not yet possessing a cardinal process; in other shells it is the place where the vertical cardinal process arises. This platform has also been called the **PSEUDOCRURALIUM**.

NOTOTHYRIUM and **NOTOTHYRIAL CAVITY**.—The dorsal counterpart of the ventral delthyrium and delthyrial cavity, *q. v.*

ORTHOCLINE.—See Pt. III, **INTERAREAS**, and t. fig. 1.

PALINTROPE.—The antero-ventrally or antero-dorsally directed shelf developed at the posterior end of the dorsal and ventral valves due to the progressive migration of the hinge margin in its growth. Formerly called cardinal area.

PALLIAL SINUSES (pl. A, fig. 13).—Extensions of the coelomic cavity into the mantle. Impressions of these sinuses are not uncommonly seen on the inside of the shell as low ridges or shallow furrows. There are usually two main trunks in the ventral valve and three in the dorsal.

PARVICOSTELLÆ.—See **COSTELLÆ**.

PAUCICOSTATE.—See **COSTÆ**.

PEDICLE CALLIST (pl. A, fig. 13).—A callus of shell substance at the internal apex of the ventral valve between the dental lamellæ, to which the postero-ventral surface of the pedicle was attached.

PEDICLE FORAMEN (pl. A, fig. 3).—A small or large round perforation at the apex or elsewhere through the deltidium for the protrusion of a small pedicle; with age, it may become large by abrasion. When this foramen is absent, the pedicle emerges between the deltidium and chilidium, or these coverings may completely close the delthyrium and notothyrium, in which case there is no known functional pedicle.

PEDICLE MUSCLES.—The muscles that retract the pedicle. In the Protremata and Telotremata, one pair originates on the ventral valve at points just outside of and behind the diductors, and another pair on the dorsal valve behind the posterior adductors (not known in orthids), while the opposite ends of both pairs are attached to the pedicle. These muscles are also called the **ADJUSTORS**. (For adjustor scars, see pl. A, figs. 12, 13, 15.) Besides these, there is an unpaired muscle, not known in early brachiopods, lying at the base of the pedicle, attaching it closely to the ventral valve.

PLANE OF COMMISSURE.—The plane passing through the anterior commissure and the hinge-line.

PLATFORM.—This term should be retained as first proposed, for the elevated and thickened muscle trace in the trimerellids. See **NOTOTHYRIAL PLATFORM**.

PLICA.—See FOLD.

PLICATE (pl. 24, fig. 5).—Used of a shell that has undulations affecting both the interior and outer surfaces. The primary ornamentation is superposed over the plications. Example: *Enteleles*.

POSTERIOR REGION.—That portion of the shell back of the transverse axis and toward the beak, or apex.

PROCLINE.—See Pt. III, INTERAREAS, and t. fig. 1.

PROTEGULUM.—The initial shell of all brachiopods.

PSEUDOCRURALIUM.—See NOTOTHYRIAL PLATFORM.

PSEUDORESUPINATE.—See RESUPINATE.

PSEUDOSPONDyliUM (pl. A, fig. 11; pl. 18, figs. 13, 14, 18, 24).—A callus resembling a spondylium, developed in some shells beneath the muscles of the ventral valve and confluent with the inner lower surfaces of the dental lamellæ. Examples: *Glossorthis*, *Finkelburgia*, *Linoporella*.

PUNCTÆ.—Any minute perforations of the test. Punctæ are here divided into two kinds: ENDOPUNCTÆ, perforations of the internal shell layer, never reaching the exterior unless the thin outer shell layer is abraded; these are the typical punctæ of the terebratulids and the Dalmanellacea. EXOPUNCTÆ, perforations that indent the external surface of the shell but do not pass through to the interior; well developed in *Paurorthis*, *Hebertella*, and *Valcourea*.

RECTIMARGINATE.—Having a straight anterior commissure.

RESUPINATE.—A condition wherein the relative convexity of the two valves is reversed, the convex ventral valve of the early growth stages becoming concave and the concave dorsal valve becoming strongly convex, producing thereby a convexo-concave shell. Strictly speaking, this condition has never been attained by the orthids, but a few genera simulate it closely, e. g., *Valcourea*, *Dinorthis*, *Plæsiomys*, *Hebertella*, etc. This latter condition might be called PSEUDORESUPINATE.

ROSTRATE.—Having a long beak, produced by narrowing of the hinge-line, as in *Conchidium*, *Cyclocælia*, etc.

SEPTUM.—See DORSAL MEDIAN RIDGE, and MEDIAN SEPTUM.

SESSILE CRURALIUM.—See CRURALIUM.

SESSILE SPONDyliUM.—A spondylium which rests directly on the floor of the valve without the support of a median ridge. Nearly attained in *Pahlenella*. See SPONDYLOID.

SHAFT.—The stalk or shaft of the cardinal process, which bears the myophore or seat of diductor muscle attachment.

SINUS.—See SULCUS.

SOCKETS.—There are sockets for articulation in both valves. In the ventral, there are two kinds associated closely with the teeth: ACCESSORY DENTAL SOCKETS, on the outside of the teeth; and CRURAL FOSSETTES OR SOCKETS (*q. v.*) on their inner sides. See t. fig. 2.

SPONDyliUM (pl. A, fig. 9).—A spoon-shaped plate, terminating more or less freely, located in the apex of the ventral valve of various stocks of articulate brachiopods. This plate serves as the seat of attachment of the muscles. It is supported by a more or less elevated, long or short, median septum. Kozłowski has recently shown (1929) that the spondylium may be divided into three different types, as follows:

SPONDyliUM DISCRETUM (pl. 14, fig. 20).—Here the dental plates do not converge and unite medially, but extend directly to the floor of the valve. Strictly speaking, this is not a spondylium, but such a condition of the dental plates is primitive and deserves a designation. This structure occurs mostly in orthids. Also see pl. 18, figs. 13, 14, 18.

SPONDyliUM DUPLEX.—See below.

SPONDyliUM SIMPLEX (pl. 7, fig. 31).—A term applied by Kozłowski to the type of spondylium in *Clitambonites*, in which the dental plates and the vertical septum are united into a single piece. This type is in contrast to the SPONDyliUM DUPLEX of *Pentamerus* (pl. 25, fig. 43), which is composed of two pieces each of which is borne on a basal septum. See PSEUDOSPONDyliUM.

SPONDYLOID (pl. 14, fig. 8).—In this condition the dental plates are so thickened on their inner basal sides that the added testaceous deposit grows together and simulates a spondylium. This contrasts with the pseudospondylium, which is formed by a callous thickening on the floor of the valve. Example: *Porambonites*.

STRIÆ.—Interspaces between costæ and costellæ. This term has been much abused and its current use for a radial rib is incorrect.

SULCUS (**SULCATE**).—A median depression in the convexity of the shell, the opposite of a fold or plica. Replaces the term sinus.

TEETH (pl. A, fig. 2).—The two articulating processes of the ventral valve. There are also accessory small teeth in the dorsal valve in many brachiopods, which are here called **DENTICLES** (*q. v.*).

TRANSVERSE AXIS.—A line through the widest part of the shell from left to right.

UMBONAL CAVITIES.—Chambers separating the dental lamellæ from the walls of the valve.

UNIPLICATE.—A term applied to the anterior commissure when there is a fold in the dorsal valve opposed by a sulcus in the ventral valve. **UNISULCATE** is the reverse condition.

UNISULCATE.—See **UNIPLICATE**.

VENTRAL DENTAL SOCKETS (pl. A, fig. 2).—Small sockets in the teeth of the ventral valve next to the hinge margin. Into these articulate small denticles on the outer wall of the dental socket. They are also called **ACCESSORY DENTAL SOCKETS**. See **DENTICLES**.

VENTRAL VALVE.—The shell situated on the ventral side of the animal, and in articulate forms having the teeth on each side of the delthyrium. Usually the larger and deeper of the two valves. **PEDICLE** and **DENTAL** are other names applied to it.

PART II. PRINCIPLES OF MORPHOGENESIS OR EVOLUTION OF FORM

NEED OF TAXONOMY

W. T. Calman, keeper of zoology in the British Museum of Natural History, says in his recent address, "The Taxonomic Outlook in Zoology,"¹ that in the days of Linnæus (1758) an experienced zoologist might have known the 4370 living species then named, but that to-day, when over 700,000 kinds have been described, the great need for the specialist is apparent. "Nothing can altogether replace that instinctive perception of affinity that comes from lifelong study" (p. 280). He goes on to say, however, that there can no longer be a "complete description" of a species, as was thought necessary by the older systematists, but that what should be done is to enumerate the essential characters in which it differs from similar forms of the genus. This address stimulated the editor of *Nature* to remark:² "There is a strong tendency to deprecate the value of taxonomy and to ignore its claims to a fair share of the attentions of scientific workers."

All animal life is subject to change as soon as the normal conditions of the environment change, and, according to Baker,³ "there is evidence that this change may not always be a matter of long years but may take place in the space of five or ten years. This statement is abundantly supported by experimental evidence. The necessity for giving names to these incipient species [ecological variants] is, therefore, obvious."

The same writer has shown elsewhere that molluscs in streams and lakes change into different forms in the course of one or two human generations, due to alterations in the environment brought about by man. If subspecies change thus quickly, paleontologists with their superabundance of time as recorded in the geological formations must expect generic change from zone to zone, and yet no genus should be made on the basis of age alone, since a genus is to be founded on the ensemble of characters as seen in one or more species.

It is said that Linnæus described in the tenth edition of his "Systema Naturæ" (1758) one genus and forty-two species of Homoptera. Now Professor Z. P. Metcalf, a student of this "small order of insects," estimates that there are known no fewer than 30,000 species distributed in 500 genera, and it is thought that there will eventually be three times as many. In this group, therefore, and in many others, it is only too plain that there can be no stability in nomenclature for a long time to come. It does not further our subject, however, to complain of the multiplicity of Nature and the consequent difficulties in attempting to give the proper name to each species under the Rules of Zoölogical Nomenclature. It is the duty of every systematist to do the best he can and let the future take care of itself. In other words, the grumblings of the anatomists, physiologists, experimental biologists, etc., are all beside the mark, since the systematist is only trying to classify what he sees in an ever changing world, namely, to determine the lines of organic descent to the uttermost ramifications possible in a stated classification that is, after all, more or less artificial. Morphology will grow and taxonomy will change as long as there are great numbers of unknown species and genera.

RISE OF BRACHIOPOD GENERA

Fabius Columna in 1616, and Martin Lister in 1678, were the first to describe brachiopods, calling them *Conchæ anomie*. Grundler in 1774 was the first to give a good illustration of a living brachiopod, *Terebratulina caput-serpentis*. Cuvier in 1792 and 1802 distinguished brachiopods from Acephala, and in 1805 gave the class its name Brachiopoda. In 1818 Lamarck knew 5 genera,

¹ Science, n. ser., vol. 72, 1930, pp. 280-284; Nature, vol. 126, 1930, pp. 440-444.

² Nature, vol. 126, 1930, pp. 461-462.

³ F. C. Baker, On Genus and Species Making. Science, n. ser., vol. 72, 1930, pp. 37-39.

including among them the operculate coral *Calceola*. In 1849 King recognized 49 genera in 16 families, and Bronn in 1862 listed 51 genera. Hall and Clarke (1892-1894) added 58 new genera and in their "Handbook of Brachiopoda" recognized 325 genera or subgenera. By 1913 (Zittel-Eastman) this number had grown to about 450, Buckman alone added 51 new genera of rhynchonellids in 1914 and now there are at least 750 genera or subgenera in good standing, in addition to some 200 rejected names, many of which will doubtless be revived. Of these 750 genera, one only belongs with certainty to the order Palæotremata, 50 (7%) are Atremata, 47 (6%) Neotremata, 234 (31%) Protremata, and 417 (55%) Telotremata. The Paleozoic has about 500 genera, the Mesozoic about 180, and the Cenozoic-Recent about 75.

THE GENUS CONCEPT

"To no human question is there an immutable and final answer."—Bather 1927

All paleontologists working to discern the genetic relations of fossils should study the Presidential Address of F. A. Bather entitled "Fossils and Life," which was delivered before Section C of the British Association for the Advancement of Science in 1920.⁴ This masterly address deals chiefly with the philosophy of ancient life in relation to that now living under the influence of the environment—the leading influence making for genetic evolution as interpreted by both paleontologist and neontologist. Bather says:

Like Botany and Zoology, Paleontology describes the external and internal form and structure of animals and plants; and on this description it bases, first, a systematic classification of its material; secondly, those broader inductions of comparative anatomy which constitute morphology, or the science of form. Arising out of these studies are the questions of relation—real or apparent kinship, lines of descent, the how and why of evolution—the answers to which reflect their light back on our morphological and classificatory systems (p. 61).

Paleontologists, unlike neontologists, are concerned with the "concept of time . . . an orderly and related succession, coextensive, in theory at least, with the whole history of life on this planet" (p. 62).

Since the days of Linnæus, biologists have sought for "natural classifications," but back of 1859 these were more arbitrary than natural; with the publication of Darwin's "Origin of Species," however, it has become more and more possible to determine the genetic relationships, or the "blood-red clue of natural affinity."

Descent, then, is not a corollary of succession. Or, to broaden the statement, history is not the same as evolution. History is a succession of events. Evolution means that each event has sprung from the preceding one. Not that the preceding event was the active cause of its successor, but that it was a necessary condition of it. For the evolutionary biologist, a species contains in itself and its environment the possibility of producing its successor (pp. 66-67). [Not until we pursue the "line upon line" method of paleontology shall we] have linked species into lineages, can we group them into genera; not until we have unravelled the strands by which genus is connected with genus can we draw the limits of families. Not till that has been accomplished can we see how the lines of descent diverge or converge, so as to warrant the establishment of Orders (p. 70).

It is undoubtedly true, as Gertrude Elles points out in her paper, "Evolutional Paleontology,"⁵ that species and genera have too often been made by paleontologists in the laboratory without the knowledge of the field, since the strata entombing fossils are the only preserved environments. Furthermore, only too often are species and genera made on the basis of chronogenesis and not on a proved genesis, and most of our genera with large assemblages of species are polyphyletic in origin.

The modern taxonomic trend based on evolution, as used by vertebrate paleontologists, is well illustrated in the paper by H. F. Osborn bearing the title "Final Conclusions on the Evolution, Phylogeny, and Classification of the Proboscidea."⁶ His viewpoint as to the value of the divisions appears, however, to be an extreme one. Here we learn that Lydekker in 1886 knew of but two

⁴ Rept. British Assoc. Adv. Sci., Cardiff meeting, 1920, pp. 61-86.

⁵ Rept. British Assoc. Adv. Sci., Liverpool meeting, 1923, pp. 83-107.

⁶ Proc. Amer. Philos. Soc., vol. 64, 1925, pp. 17-35.

genera, *Elephas* and *Mastodon*, and that not so long ago all vertebrate paleontologists regarded the Proboscidea as a monophyletic line. Osborn, according to his "phylogenetic classification," now divides the "phylum" Proboscidea into at least 16 races or lines of descent. These he arranges into 4 orders, 5 families, 13 subfamilies, 28 genera, and 290 species.

A. Morley Davies in his preface to Sahni's very careful study of the terebratulids of the British Chalk,⁷ a work wrought out along the best modern lines, has the following to say regarding the most reliable generic characters in brachiopods:

Internal structure has proved the surest clue to relationship. Beecher and others based the classification of the "long-looped" Terebratellids primarily on the form and development of the brachial loop; Buckman relied on the muscle-scars in the case of the Jurassic Terebratulids and Rhynchonellids . . . Once the definite clue has been found by which distinct stocks can be separated, it becomes possible to discriminate among the multitude of seemingly random external variations. Some of them, either individually or, more frequently, in particular associations, are definitely correlated with internal features and become diagnostic for particular stocks: they belong to what Douvillé has termed . . . "static characters," persisting or slowly changing as evolution proceeds. Others are among Douvillé's . . . "progressive characters," which go through a series of stages often parallel in different stocks. It is these parallel developments, sometimes predominating over the static characters so as to effect a "convergence" or homœomorphy between different stocks that are most apt to mislead in hasty determination. Yet these progressive characters may sometimes remain relatively static for a period, so as to serve provisionally or partially as diagnostic characters (pp. v-vi).

When Sahni began his work there were 14 Upper Cretaceous species usually referred to *Terebratula*. It now appears that not one of them belongs to this genus, his memoir defining 57 forms in 12 new genera! This shows what must be done nowadays if one's work is to stand. One must lift the covers and delve into the insides for the most reliable characters, and then carefully examine the covers to discover the homœomorphs and the significance of the slight changes in external form.

Among students of brachiopods, none has more clearly set forth the best present methods of determining the genus from the genetic standpoint than J. Allan Thomson.⁸ He says:

Biological classification is now an attempt to express the degrees of affinity through descent [italics ours]. Instead of as few characters as possible being used to decide upon the generic position of a species, as many characters as are necessary are employed to determine the relationship to other species. It has frequently been found that the species grouped together under the older wide genera form homœomorphous series of polyphyletic origin—i. e., their similarity of form has been attained through different lines of dissimilar ancestors (p. 120).

According to Buckman (1918),⁹

Generic division will not be complete for scientific purposes until all polyphyletic series are rightly separated. If the criteria now obtained are insufficient for this work of separation, it is the task for future observers to note and to utilize other characters (pp. 133-134).

Thomson says, further:

Another change in the conception of the genus has resulted from a fixation of procedure in regard to the law of priority . . . It has become necessary to define each group not only by an assemblage of characters originally proposed for it by its author, but by a type within the group with which the affinity of other members may be compared—a species by a type specimen or holotype, a genus by a type species or genotype, a family by a type genus (p. 121).

The genetic work of paleontologists must be guided, however, by the results of the neontologists, who have the living organisms to study in their entirety, but even among them the demonstration of lines of descent lies with the experimentalist. The work of these biologists shows how deceptive "blood-relationship" may actually be. In this connection we may summarize here the con-

⁷ M. R. Sahni, *The Terebratulidæ of the British Chalk*, Mon. Paleontog. Soc., 1927, 1929.

⁸ *Brachiopod Morphology and Genera (Recent and Tertiary)*. N. Zealand Bd. Sci. and Art, Manual No. 7, 1927.

⁹ *The Brachiopoda of the Namyau Beds, Northern Shan States, Burma*. Geol. Surv. India, Pal. Indica, new ser., vol. 3, mem. 2, 1917 (1918).

clusions of the experimental ecologists H. M. Hall and F. E. Clements, as related in their monumental monograph of 1923.¹⁰

The basis of this monograph lies in "experimental and quantitative methods," and the experiments to be conclusive "must extend over a long period of time." The authors have taken many species of sagebrush and transplanted them from one environment into another, for example, interchanging one growing in a dry environment with another at home under wet conditions, and this divergence in habitats gives opportunity for convergence in characteristics that "may sometimes become practical identity." From these experiments they got results that led them to revise the species of three genera as follows:

| Genus | "Species" up to 1923 | Present divisions | | | |
|----------------------|----------------------------|-------------------|-----------------|---------------|--------------------|
| | | "Sections" | "Major species" | "Sub-species" | "Minor variations" |
| <i>Artemisia</i> | 125 | 4 | 2 | 29 | 120 |
| <i>Chrysothamnus</i> | 88 | 4 | 12 | 40 | 44 |
| <i>Atriplex</i> | 103 | ? | 47 | 37 | 70 |

Let us look a little more deeply into what these experimentalists have to teach us: Taxonomy in biology, as the word indicates, is

the science of arrangement or system, and hence classification [of the organic entities. Naming of species is but the first step in taxonomy, and even their description is not the whole of this science, since taxonomy should mean the placing of the species in nature's lines of descent; or, stated in another way, the placing of them so as to give] the best possible record of evolution and relationship. . . . Absolute adherence to phylogeny should be the basis of classification. . . . Evolution is the process and phylogeny the record of descent.

Taxonomy leans most heavily upon morphology, and should bring to its aid not only histology and physiology, but ecology and genetics as well.

Indeed, if it [taxonomy] is to reflect evolution as accurately as it should, it must regard physiological adjustment as the basic process, and morphological and histological adaptations as the measurable results. This means that the taxonomist of the future will think in terms of evolutionary processes, and will learn to treat his morphological criteria as dynamic rather than static. [Quantitative ecology] traces the evolution of new forms in minute detail, in so far as they arise through adaptation or variation, and consequently furnishes the only direct evidence of relationship by descent. It affords the sole method of testing the manifold assumptions of existing taxonomy, and provides the foundation upon which an objective and permanent taxonomy may be reared.

At present, however, taxonomy is more often the artificial expression of organic evolution; artificial because the science is as yet mainly one of personal opinions, and naturally this is more true in paleontology than it is in neontology.

A natural classification must maintain as well as reveal the different degrees of relationship as expressions of different stages of evolution, and it can do this most accurately with genera, sections, species, and variads, where the lines of evolution are still in a condition conducive to experimental study Since the limits of orders and families are determined by genera, and the limits of genera by species, the whole problem resolves itself into a statistical and experimental study of species and their evolution (pp. 3-6).

It is now common practice to regard the genus merely as a concept, and often as an artificial one. Regarding this, Hall and Clements say:

This is doubtless true for those who regard the genus merely as a pigeon-hole, chiefly convenient for the filing of new species. Such a view has its justification in the usual practice of making genera. . . . It is not sup-

¹⁰ The Phylogenetic Method in Taxonomy. The North American Species of *Artemisia*, *Chrysothamnus* and *Atriplex*. Carnegie Institution of Washington, Pub. No. 326. See also Clements, An Ecologic View of the Species Question. Amer. Nat., vol. 42, 1908, pp. 253-264.

ported by the evidence drawn from the methods of evolution or the record of phylogeny. To the student of evolution, the genus represents a certain characteristic portion of the line or field of specialization, and its existence is as definite as that of the species which constitute it. . . . As a consequence of the unrestricted play of personal opinion, not infrequently aided by bias or carelessness, present-day taxonomy contains genera of every possible quality. Many of these disappear completely when the test of evolution is applied to them (p. 6).

In paleontology, more than in neontology, genera are not uniform in differentiation; one stock will vary but little while another will do so extensively. The genera with but one or a few species will practically take care of themselves, but in those with a great number of species it is desirable to name all the determined genetic lines, since evolution is the *process* and taxonomy the *method* of marking the phylogenetic lines of descent.

It is clearly recognized that the making of new genera is purely a matter of personal judgment at the present time. . . . There is no general agreement as to criteria, methods, or results, and the importance of evolution as the one safe guide is rarely if ever considered. A knowledge of the genus as a whole, especially when it includes exotic species, is too often lacking, and little or no thought is given to the phylogeny of the genus and its sections in relation to genera of the same evolutionary stock. . . . It would seem desirable to make rather more of sections as records . . . of specialization within the generic stock (pp. 8-9).

PALEOECOLOGY

The paleontologist should study his specimens and species primarily in the light of the field to learn their environmental and biotic relations, since the strata of their entombment are the habitats of fossils. We hold with Clements¹¹ that the habitat is

the motive force in the life processes of plants and animals, both as individuals and as communities. . . . Ecology deals primarily with processes and is inherently and universally dynamic . . . quantitative in method, beginning with the habitat in which measurements are relatively simple, and running through individual and community responses in which they are difficult (p. 369).

As paleontologists we should, therefore, be primarily interested in the habitat of fossils and of our faunas, since organisms are "the end forms of responsive processes." In other words, it is seemingly the environment in the main that brings on the organic responses seen in the development and evolution of fossils; accordingly the paleoecology and the time factor of our faunas should be considered in addition to the morphology, in the making of species and genera.

In paleontology we have, it is true, but a small part of the whole of the habitat or of the bios, and therefore it is "puzzling to understand how the demands of ecology can be met in a field where processes have ceased. The readiest answer, and a fairly complete one, is afforded by the *principle of uniformity of processes* [italics ours], the use of which has made modern geology possible" (p. 370). Accordingly we paleontologists can learn much from the ecologists, but most from the entombing strata and the associations of the fossil faunas.

In the paleoecology of marine faunas, the main factors in conditioning the local biotas are the interrelations of temperature, currents, nearness to shore, and nature of sea bottom; depth, chemical content, and clarity of water; prevalence of bottom-living flora, nature of floating life, presence of oxygen as food, penetration of sunlight, and interaction of life.

HOMŒOMORPHY

What has long been known as "parallel development" has had but scant notice among American students of brachiopod ancestry, Beecher¹² being about the only one to pay attention to this principle of mimicry of outer form; among the ammonites, however, the factor has been used a great deal since its introduction by Alpheus Hyatt and its later acceptance by J. P. Smith. In Europe, Buck-

¹¹ Scope and Significance of Paleo-ecology. Bull. Geol. Soc. America, vol. 29, 1918, pp. 369-374.

¹² C. E. Beecher, Some Correlations of Ontogeny and Phylogeny in the Brachiopoda. Amer. Nat., vol. 27, 1893, pp. 599-604.

man¹³ applied the principle of parallel development for many years and chiefly among the Jurassic ammonites and brachiopods; and his work and now ours show that external characters are not always reliable for generic and phyletic studies. The application of this principle to the genera heretofore described often plays havoc not only with them, but above all with our notions of their genetic relationships.

This phenomenon of parallel development Buckman has called *homœomorphy*. It refers to species nearly alike so far as superficial appearance is concerned, but unlike when particular structural details are closely examined. It is the phenomenon of similarity in general with dissimilarity in details, [or] the tendency of different genetic stocks to pass, quite independently, through similar phases of development . . . There is a tendency among Jurassic Brachiopoda for independent non-plicate species to become multiplicate . . . and in the Rhynchonellidæ for the multiplicate (costate) to become spinous (*Acanthothyris*), and in certain cases a spinous species may, with age, retrogress to lose spines.

The various species of different stocks may either produce these developmental characters more or less contemporaneously, in which case such forms are called *isochronous homœomorphs*, or they may produce the characters at different dates—a later form simulating an earlier one—in which case they are called *heterochronous homœomorphs* (1901, pp. 231-233).

In the Jurassic of the Cotteswold district of England, in rocks of about the same date, there are five independent developments of the same character among species of Terebratulidæ. In nearly related stocks much excuse may be made for errors in identification, but when such errors occur in different families whose internal structural details are quite distinct, then "the confusion of two species of these families under one name becomes serious" (p. 239). In fact, among the Jurassic terebratulids and rhynchonellids, homœomorphs are so common that "they may be said to form veritable 'traps' in the matter of identification" (p. 262).

Extraordinary homœomorphs occur among the lobate terebratulids (*Pygope*, *Antinomia*, *Pygites*) and these are set forth by Buckman in his paper of 1906.

When Hall and Clarke prepared their monograph, the perplexing feature of homœomorphy was not clearly understood, consequently some genera were made on the basis of external form alone. It has been found in the present work that no one character, either internal or more especially external, can be relied upon in the identification of a genus, but that a genus must be characterized by a combination of these features. Among the orthids there have been convergences either toward other orthid families or toward the external form of other groups. *Productorthis* of the early Ordovician may be cited as a conspicuous example in its resemblance to the productids of the late Paleozoic. There are three genera that ape the external form of *Skenidium* (*Skenidioides*, *Mystrophora*, *Hesperorthis?* (*merope*)), and no fewer than seven have the external form of *Pionodema* (*Mimella*, *Hemipronites*, *Doleroides*, *Deltatrete* (some species)), *Finkelburgia*, *Schizophorella*, and early *Schizophoria*.

Of interest in this connection is the accelerated development of the Ordovician Clitambonitidæ of European Russia. Early species took the outside features of *Strophomena*, as in *Gonambonites*, and some of these later aped forms of *Hebertella*. *Hemipronites* is much like a *Pionodema*, and *Vellamo* has essentially the form of *Hesperorthis*. This diverse development occurred in a relatively short time, and the whole stock perished with the Ordovician.

¹³ S. S. Buckman, Homœomorphy among Jurassic Brachiopoda. Proc. Cotteswold Nat. Field Club, vol. 13, 1901, pp. 231-290.

Brachiopod Homœomorphy: *Pygope*, *Antinomia*, *Pygites*. Quart. Jour. Geol. Soc., London, vol. 62, 1906, pp. 433-454.

Brachiopod Homœomorphy: *Spirifer glaber*. Ibid., vol. 64, 1908, pp. 27-33.

PART III. MORPHOLOGY OF THE ORTHOID SHELL

The Orthoidea, to be described in more detail later, are a prolific stock of primitive Protremata which persisted, according to our present knowledge, from the middle part of the Lower Cambrian to the end of Permian time. They are rather primitive brachiopods, certainly the simplest of the "articulate" stocks, and are characterized by more or less strongly developed interareas in both valves. Primitively the delthyrium was covered by a deltidium, but in later progressive stocks this structure was lost and the delthyrium was unmodified except for lateral plates or sporadic apical plates.

This large suborder may be divided into two superfamilies on the basis of the shell structure, whether fibrous and endopunctate or fibrous and impunctate. With these superfamily characters go definite internal structures that are described in later pages.

Most of the Orthoidea described in this volume were, at one time or another, classified under the generic term *Orthis*. Even as late as 1892, the date of Hall and Clarke's great revision, not more than thirteen orthoid genera were in use. These authors showed that *Orthis* (1828) had become a "dump" genus, and that it embraced at least 13 groups of shells with orthoid features, besides 10 other old or new genera with related forms. They further blazed the way toward a correct genetic understanding of Paleozoic genera, a method that has been followed ever since and one that has guided us in turn in the present revision. Schuchert (1897) regarded Hall and Clarke's "groups of *Orthis*" as genera, and in the Bibliography of Schuchert and LeVene (1929) there are catalogued as of July 1928 52 accepted genera of orthoids. In the present volume we recognize 103 genera or subgenera (29 are new) constituting the superfamilies Orthacea, Clitambonacea, and Dalmanellacea. These statistics show also the accelerated rate at which students of brachiopods are discerning the genetic ramifications of the orthoids.

We believe that the present arrangement shows genetic relationships more clearly than heretofore and that our classification is more natural. But it can not be final as yet, and as years pass, greater refinement in paleontologic and stratigraphic practice, along with the making of additional collections from old fields and new, will enlarge our knowledge and tend to alter our scheme. We hope, however, that our fundamentals are sound and that time will fill in either the details of the scheme here presented or that of nature, since after all we are striving to learn nature's ways of creation.

MORPHOLOGY OF THE EXTERIOR

ORIENTATION OF THE SHELL

In citing directions in or on a brachiopod shell, we shall use the terms dorsal and ventral, and anterior and posterior (pedicle end). When discussing or figuring the posterior of a brachiopod, we place the ventral valve down, as this is the correct biological orientation in the living animal. The terms ventral and dorsal, therefore, indicate the vertical direction. In other words, these directions are at right angles to the plane of the commissure, which is oriented by us in a horizontal direction. The terms anterior and posterior, on the other hand, define directions parallel to the plane of the commissure. These terms can therefore be applied with precision regardless of orientation, and thus enable us to avoid the ambiguous terms front and back, down and up.

In describing the shape, contour, or profile of a shell, the writers are following Thomson and Buckman in giving preference to the dorsal valve. This leads to the use of an unfamiliar term for some shells which are commonly called concavo-convex, as *Dinorthis*; according to our usage this is a convexo-concave shell. No matter which valve be taken for reference, any precise nomenclature must recognize a convexo-concave stage as well as a concavo-convex one. For the sake of uniformity, then, we have adopted the scheme used by these two authorities on Mesozoic, Cenozoic, and Recent brachiopods.

COMMISSURES

When viewed from the front or anterior, the line of contact of the two valves is primitively straight but in most derived genera it is more or less undulated. The same holds for the lateral commissure. Buckman has analyzed the flexures of the anterior commissure in Mesozoic rhynchonellids and terebratulids, and has named nine stages developed out of the primitive straight or rectimarginate one. Among the orthids only two of the Buckman stages can be recognized, namely the sulcate and uniplicate ones; both of these are the simplest of the modifications of the rectimarginate stage. In the *sulcate* stage there is a single sulcus in the dorsal valve and a fold in the ventral, as seen in *Aulacella*, *Enteletina*, or *Parenteleles*. This type of commissure is rather uncommon. In the *uniplicate* stage, these conditions are reversed and there is a single fold on the dorsal valve and a sulcus in the ventral one. This is the more common condition and is well exhibited by *Platystrophia*.

The conclusion that a fold and sulcus, or what amounts to trilobation, may have been developed to facilitate the passage of the incurrent and excurrent streams of water used in the aeration of the mantle and for food-gathering was advanced by Orton.¹

The tendency to develop a fold and sulcus is inherent in most Orthoidea but in some of them, for example *Hebertella*, there is little stability as to which valve shall receive the sulcus. In some stocks there is a marked reversion of the fold and sulcus, as in *Eridorthis* and *Thiemella*.

The common condition of the lateral commissure is a more or less strong flexing toward the dorsal valve. This is true of *Valcourea* and many other forms. The primitive condition is an unflexed lateral commissure. A ventrally flexed lateral commissure is rare.

CONVEXITY

In the Cambrian, most shells are normally biconvex, as is the first shell growth in all brachiopods, and here it is also usual to find the ventral shell the more convex and the deeper. In later forms the reverse condition is, however, of common occurrence and is independently originated over and over again.

The great majority of brachiopods, viewed in longitudinal section, are biconvex, in that the external curvature of both valves is convex, with the ventral the more so and therefore deeper than the dorsal. This common condition is called the *lenticular* or *biconvex phase* by Buckman. More rarely it is the dorsal shell that is more convex, and such forms can be described as *dorsi-biconvex*.

Resupination is a condition that has been reported commonly in the orthids, but unfortunately the term has never been defined with any precision. Some authors regard brachiopod shells as resupinate when the ventral valve has less volume than the dorsal. *Atrypa* would be a fine example of such "resupination," but this is not what the term apparently meant originally. As applied by Hall and Clarke, it embraces such shells as have the ventral valve concave and the dorsal convex. According to this view, *Valcourea* and *Strophomena* would be two unrelated examples of resupination. However, there is a marked difference between *Valcourea* (and all other convexo-concave orthids) and *Strophomena* in the manner of the reversion of convexity in the ventral valve. In the young stages of *Strophomena* the ventral shell is convex and may carry a low fold; the dorsal valve is essentially flat and may be gently sulcate. In later stages, however, the dorsal shell becomes strongly ventricose and the ventral one deeply concave. In the convexo-concave stage of the orthids, on the other hand, as in *Valcourea* and *Hebertella*, the dorsal valve never has the incipient flat stage as seen in *Strophomena*, and this affords an easy external way of distinguishing a strophomenid from an orthid homœomorph. Consequently in this work we are restricting the term *resupination* to the condition seen in *Strophomena* and its allies, while the other condition among orthids may be called *pseudoresupination*.

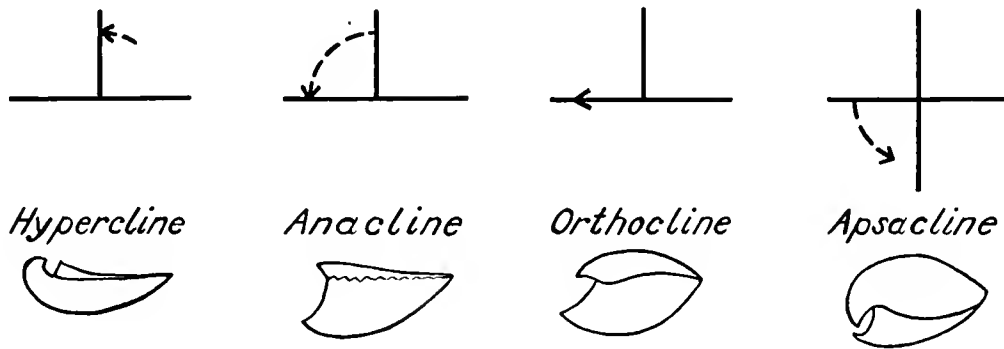
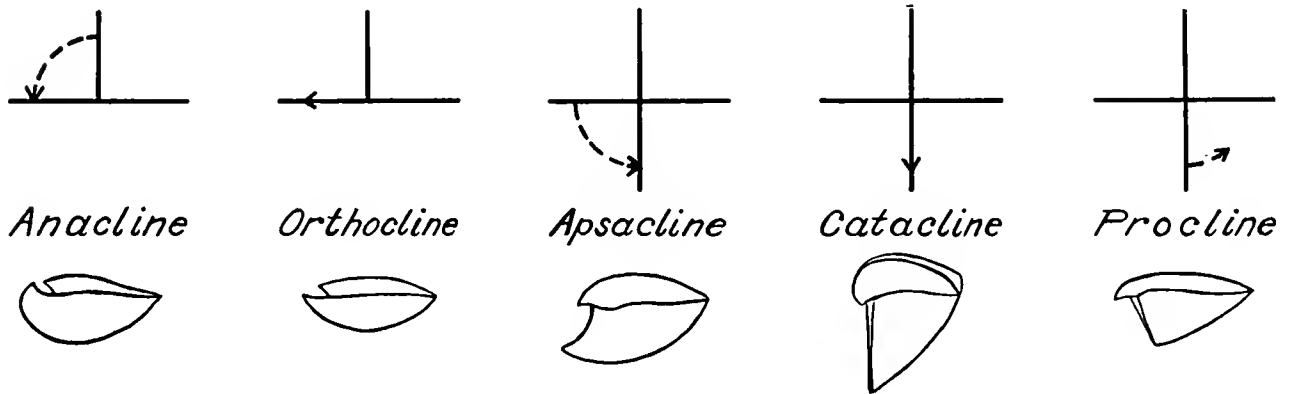
¹ Orton, J. H., On Ciliary Mechanisms in Brachiopods and some Polychætes. Jour. Marine Biol. Assoc., U. K., new ser., vol. 10, 1914, pp. 283-311.

INTERAREAS

According to Buckman,² the word *area* should be retained for general use, but *interarea* might be used for "the area lying between the apex and the posterior line of valve-junction—the cardinal margin when there is a hinge, but at any rate the posterior margin."

Interareas, or what were formerly called cardinal areas, are usual in most of the members of the order Protremata and especially in its most primitive stock, the Orthoidea. True interareas are

VENTRAL



DORSAL

FIG. 1.—Diagram to show various positions of the interarea with relation to the plane of the commissure.

at times also well developed in the Telotremata, but never in the Atremata or Neotremata. When a similar structure is present in the two last named orders it is due to holoperipheral growth or to subsequent internal thickenings of the posterior margins, and in both these instances it is termed a *pseudointerarea*.

The interareas are, then, the plane or slightly curved surfaces of the palintrope, which is a shelf, growing antero-ventrally or antero-dorsally according to the valve, and representing the progressive growth track of the hinge-line or plane of articulation. In describing or discussing the inter-

² Brach. Namyau beds, 1917 (1918), p. 453.

area the writers consider the length of said surface to be in the same direction as the length of the valve. The width of the interarea is the width of the hinge-line. The length of the interarea is thus seen to be perpendicular to the width or perpendicular to the hinge-line. Ordinarily the ventral interarea has the greater length.

An interarea may be plane or more or less markedly concave. It may be striated parallel to its length or to its width or both, most interareas having striae of one kind or another. The horizontal striae are commonly growth-lines; the vertical striae may represent the growth tracks of accidental irregularities that make, as it were, "teeth" along the hinge-line. More uncommonly the interareas may be ornamented by fine elevated lines passing obliquely across the surface from the beak, as in *Polytæchia* and *Deltatreta* (see pl. 6, fig. 14).

Another important feature of the interareas is their inclination from the plane of the commissure, which may cause important modifications of the muscle marks, the dental plates, and the cardinalia. When studying the inclination of the interareas the ventral valve is placed by us below the horizontal and the beaks (arbitrarily) on the observer's left. The plane of the commissure is then horizontal and the dorsal valve is up. In this orientation the following positions may be observed:

Ventral valve: (a) *anacline*—between vertical and horizontal—ex. *Orthis s. s.*; (b) *orthocline*—interarea horizontal—ex. *Archæorthis*; (c) *apsacline*—between horizontal and vertical, 90° - 180° from erect vertical—ex. *Hesperorthis*; (d) *catacline*—bent down 90° from the horizontal—ex. some species of *Clitambonites*; (e) *procline*—interarea bent more than 180° from the vertical—ex. *Dinorthis* (*Retrorsirostra*). In the dorsal valve the anacline, orthocline, and apsacline conditions are recognized, and in addition, a *hypercline* condition in which the interarea is rotated in an anterior direction more than 90° (see t. fig. 1).

This nomenclature has the advantage of enabling the observer to state precisely the average or individual inclination of either interarea, or, if he desires to be more specific, the number of degrees subtended by the interareas or by either interarea and the horizontal. For example, one may define a certain interarea as 30° apsacline.

Of interest in connection with the interareas is the presence of a narrow triangular space on either side of the delthyrium or notothyrium. One side and the base of the triangle are formed by the delthyrial margin and the hinge-line, respectively. The other side is defined by a line running from a point outside of the tooth in the ventral valve, or the socket in the dorsal valve, to the beak. This line represents a suture marking the progressive growth of the tooth and socket; it is the line between new shell deposited on the tooth or in the socket against the old shell of the hinge-line during the growth of the valve. In the Strophomenacea a similar triangular space has been called the "secondary area," but in these shells, *Derbyia*, *Orthotetes*, etc., the outer or suture line is never correlated with either the teeth or the sockets. It is very doubtful, then, if this better known and much discussed secondary area of the Strophomenacea can be homologized with the similar-appearing structure in the orthoids.

DELTIDIUM

MODIFICATIONS OF THE DELTHYRIUM (DELTIDIUM).—The deltidial covering has for many years received much attention from taxonomists, and the kind of covering is now thought to determine the order to which the different groups of brachiopod shells belong. The deltidium³ is an arch

³ According to Hall and Clarke (Pal. N. Y., vol. 8, pt. I, p. 189, footnote), "The term *deltidium* was proposed by von Buch for the triangular plate which, in many articulate genera, covers more or less completely the space between the outer margins of the dental ridges. This plate he describes as composed of two pieces which may either completely surround the foramen (*deltidium amplexans*), bound it on its lower side (*deltidium sectans*), or the parts may be separated for their entire length by the foramen (*deltidium discretum*). These component parts of the deltidium take their origin from the margins of the triangular cavity beneath the beak, but in some genera, particularly in *Strophomena*, *Spirifer*, and their allies, there is still another form of shelly plate which grows from the apex downward, and to this the term *pseudodeltidium* was applied by Bronn. Among recent writers there has been considerable laxity in the use of these terms and it is very doubtful if they can be applied with precision."

In the present work we have preferred to follow Hall and Clarke, Beecher, and others in using the term deltidium, applying it, however, to the cover composed of a single piece which restricts the delthyrium of the Protremata.

built with its piers against the angle formed by the palintrope and the dental plates. The piers are usually buttressed against the track or axis formed by the growth of the tooth (see D, Pl. A). The attachment is strengthened by adventitious deposit laid over the whole inner surface and along the sides of the dental plates and usually concealing all sutural contacts. Externally the interarea and deltidium appear to be continuous and a suture is rarely visible unless the deltidium is somewhat broken in. Shells having lateral plates in addition to the deltidium, however, commonly show suture lines (see below) where the lateral plates overlap the deltidium. In the *Clitambonitidæ*, and in the older *Billingsellidæ* as well, it is not uncommon for the deltidium to carry an axial stiffening along its inner surface. Hence the deltidium is a distinct plate, deposited in all probability by the mantle, and is not a part of the palintrope or cardinal area. It is therefore not homologous with the homœodeltidium, as stated by Walcott and Schuchert—a change of opinion of very great significance in classification.

In *Hesperorthis* the deltidium, or “apical plate” as it has commonly been called, is truly an arch as in *Clitambonites*, and its piers are also built against the sides of the delthyrial cavity. Since *Hesperorthis* commonly has in addition lateral plates or extensions of the palintrope over the margins of the delthyrium, the deltidium rarely is arched above the interarea. On the other hand, the deltidium of *Hesperorthis* has been homologized with the apical plate of *Spirifer*. In *S. arenosus* and many other forms of the genus *Spirifer* (*sensu lato*), the so called apical plate is a callosity filling the back end of the notothyrial cavity but rarely if ever attaining the level of the interarea. It is not a deltidium as in *Hesperorthis*, and accordingly the various structures are not homologous, although they probably serve the same purpose, that of pedicle attachment.

In a few of the punctate orthids or Dalmanellacea, apical plates have been noticed. They are especially well developed in the Schizophoriidæ and *Parmorthis*, but in no wise do they suggest a deltidium as defined above. The structure is not an arch, but a flat plate flush with the interareas. In *Pionodema* the anterior portion of the plate is concentrically lined and bevelled sharply below the level of the interarea, suggesting that this small structure served the same purpose as the pedicle callist. *Mystrophora areola* also has a flat plate, but here it lies beneath the level of the interarea.

The deltidium may or may not be perforate at the apex. In some species of *Billingsella* there is a minute perforation barely large enough for the passage of a hair. The resemblance of this apical foramen to that seen in the Strophomenacea has been urged as one link of kinship between the two groups. There are, however, no other anatomical or stratigraphic grounds to support this supposition, but whenever this apical foramen occurs it is assumed either to have functioned for the protrusion of a pedicle, reduced in these forms to a mere thread, like the byssal threads in some lamelli-branches, or to have furnished passage for the anus.

In one large group of shells, the Clitambonacea (pl. A, fig. 3), there is commonly a conspicuous apical foramen which undoubtedly served for the passage of the pedicle. Distinct scars of pedicle attachment have been observed in *Deltatrete* on the under surface of the deltidium and the floor of the delthyrial cavity. In *Clitambonites* and *Estlandia marginata*, the foramen is sealed at maturity by shell substance deposited within it (see pl. 8, fig. 8). This clearly means the loss of a functional pedicle in later mature life.

FUNCTION OF THE DELTIDIUM.—The function of the deltidium in all brachiopods is as yet not clearly understood, since our studies do not embrace the Strophomenacea wherein this structure has its best development. From the fact that the deltidium is present in the oldest and most primitive forms, we must conclude, however, that it had some functional importance to the brachiopod possessing it. In the geologically younger species, where the deltidium is almost uniformly absent, life without the structure was obviously possible. At first it appears difficult to understand the value of a structure such as the well developed deltidia in the Strophomenacea, where, by their forward growth, the pedicle opening will be constricted more and more, and in some forms no opening at all will be left for the protrusion of the pedicle (*Stropheodonta* of the strophomenids); whereas in other genera the deltidium has been resorbed or not allowed to grow by a thickened and therefore more vital pedicle. This problem is of great interest, and may be solved when the great line of deltidium-bearing shells, the Strophomenacea, are restudied from this point of view.

Among the Orthacea we note, however, the interesting fact that in some species of *Valcourea*

the deltidium is a normal and well developed structure, while in other species of the same genus it is completely wanting. In the species without a deltidium, there is a well marked pedicle callist or triangular scar which probably is the seat of pedicle attachment (see pl. 10, figs. 19, 22, 24). This evidence appears to indicate that there is some connection between the deltidium and the pedicle. It has been observed, further, that in orthid species having a deltidium, such as *Hesperorthis tricentaria*, *Dinorthis sweeneyi*, *Valcourea*, and others, the adductor and diductor muscles occupy the entire delthyrial cavity, but in these forms there is no vestige of a pedicle attachment. Hence if there was a functional pedicle, it must have been attached to some portion of the deltidium. These observations were anticipated years ago by Winchell and Schuchert,⁴ who clearly expressed the same views, as follows:

In all the species of *Orthis* observed when a pedicle muscle [callist] is present a deltidium is absent; but where this plate is developed the muscle [callist] is rudimentary. This evidence leads the writers to the conclusion that the pedicle muscle is attached to the bottom of the valve in the apex of the delthyrium when the deltidium is wanting, but when it is developed the muscle is then more or less attached to the deltidium.

In shells provided with a deltidium of the *Deltatrete* type, and having a prominent foramen, it has been determined, at least for *Deltatrete*, that there is a well marked, even conspicuous pedicle callist in the apex of the delthyrial chamber. Punctate shells are usually not provided with a deltidium, but when an apical plate is present, as in *Pionodema*, its position in the valve and the lack of any visible scar of pedicle attachment on the floor of the delthyrial cavity make it clear that this plate served for pedicle attachment.

LATERAL PLATES.—In many genera, especially those of the Orthidæ, there are lateral plates which restrict the delthyrium. Such are prominent in *Glossorthis* (pl. 4, fig. 28) and *Ptychopleurella* (pl. 6, fig. 9). Perhaps the best example is *Glossorthis*, in one specimen of which the right plate has been fractured slightly, emphasizing the suture line. In *Hesperorthis* the ventral shell has not only these lateral plates but likewise a small deltidium, showing the close connection of these different parts of the same structure secreted by the mantle. These lateral plates strongly resemble deltidial plates in manner of growth and position. They apparently grow inward and forward by marginal deposits of the mantle, since they show successive growth-lines as in deltidial plates. They have, however, never been observed to meet and in this respect are not unlike incomplete deltidial plates of certain of the Rhynchonellacea and Terebratulacea. These observations appear to us very important as bearing on the source of deltidial plates in the order Telotre mata.

Less well developed plates of the sort described above occur also among the Pentameracea and they have received considerable attention by other students of brachiopods. Hall and Clarke describe them in several genera, and Kozłowski has gone so far as to place the Pentameracea in the Telotre mata because of their presence in that group.

MODIFICATIONS OF THE NOTOTHYRIUM (CHILIDIUM AND CHILIDIAL PLATES)

In the dorsal valve the covering of the notothyrium is termed the chilidium. This structure is usually absent in post-Cambrian orthids but occurs sporadically (probably as re-developments) or in modified form in later genera. The usual type, seen in *Vellamo*, is a convex, perforate arch built with its piers against the margin of the notothyrium and with the suture line of contact commonly healed or grown over so that the interarea and chilidium appear continuous. The outer surface of the arch is marked by convex lines or thin lamellæ of growth. On the under side of the chilidium the attachments to the sides of the notothyrium are strengthened by callus deposit laid over the points of contact and along the walls of the notothyrial cavity. In many species of the Clitambonitidæ the posterior surface or edge of the cardinal process is attached to the under or anterior surface of the chilidium. This type of notothyrial covering occurs throughout the Billingsellidæ and Clitambonitidæ. It is also present in some genera of the hesperorthid tribe.

⁴ Geol. Minnesota, vol. 3, pt. 1, 1895, p. 422.

In endopunctate orthid shells modifications of either the delthyrium or notothyrium are of uncommon occurrence. Only one instance of a true deltidium is known and that is in *Kayserella*, which stands unplaced in the Orthacea. A chilidium is also known in *Heterorthis* (see pl. 20, fig. 19). It is strongly convex and arches over the carinate postero-dorsal portion of the carinate median lobe of the cardinal process. The only suggestion we can offer in regard to its function is that it serves for protection of the muscle attachments on the cardinal process.

Of unusual form and interest is the umbrelliform chilidium of *Productorthis* (see pl. 4, figs. 15, 16). This plate has its origin in the growth of two discrete plates along the notothyrial margins. These grow dorsally to the dorsal surface of the cardinal process, uniting and expanding into a circular plate that hangs over the distal end of the process like a small umbrella. Here again the function may be one of protection for the muscle attachments.

In some orthids there occurs an incomplete chilidium or what may be termed *chilidial plates*. These are low plates projecting posteriorly from the notothyrial margins and forming low walls on each side of the notothyrium. These chilidial plates are commonly thickened by callus deposit on the interior and cemented firmly by the spread of callus covering all points of contact. Chilidial plates characterize *Nicolella*, *Deltatreta*, *Pomatotrema*, and *Planidorsa*.

From the above, it appears that the sporadic reappearance of the chilidium and chilidial plates in late forms cannot have a direct genetic linkage with the older genera wherein these structures are of continuous development; the former suggest, rather, atavistic returns of primitive features. In the Clitambonitidæ, where the normal genera possess a chilidium, its persistent absence in other forms must mean a progressive change of considerable significance in establishing species and genera, for example in *Apomatella*.

MORPHOLOGY OF THE VENTRAL INTERIOR

ARTICULATION

Genuine articulation is well developed in all of the Orthacea of the Cambrian, and its origin is therefore to be sought in the most primitive order, *Atremata*.

In the orders *Atremata* and *Neotremata* the two valves are held in apposition by muscles, but in the *Protremata* and *Telotremata* they are held in place by teeth and sockets and sometimes by other articular devices that together act as hinges. In many forms the brachial process or brachio-phore also assists in locking the valves, since it articulates with the tooth of the ventral valve and helps to prevent lateral motion.

It will be shown directly that the tooth of the ventral valve in Orthacea bears a socket on its posterior surface and a fossette on its inner and dorsal face. The accessory socket of the posterior surface receives a small denticle on the outside of the socket of the ventral valve and the tooth fits into the dorsal socket. On the other hand, it will be shown in the discussion of sockets that the crural fossette receives the carinate or expanded posterior edge of the brachio-phore. Accordingly, we see that the brachio-phore is as important in the articulation of these brachiopod shells as the tooth and socket.

TEETH.—Teeth and dental plates are unknown in the inarticulate orders *Atremata* and *Neotremata*, but ventral teeth with their dorsal sockets are present in all the Cambrian genera of the Orthacea, though they appear to be very rudimentary in *Kutorgina*, thought to be the most primitive genus of the articulate order *Protremata*. On the other hand, dental plates are not always present in the older Cambrian genera (absent in *Nisusia*), but later on they make their appearance and are then usually present.⁵

The teeth or articulating apophyses are situated immediately laterad of the margins of the delthyrium, or, in a few genera, at the intersection of the delthyrial margin and the hinge-line. When viewed from the posterior, the teeth are roughly triangular in outline, the apex of the triangle being

⁵ Walcott, Camb. Brach., 1912, p. 310.

directed toward the delthyrium. The teeth are considered to extend ventrally as far as the ridge bounding the crural fossette (see below) on the inner face of the tooth. The progressive forward growth of the tooth produces a thickening under the palintrope along the delthyrial margin, and likewise a triangular area on each side of that margin. This small area is bounded on the inside by the delthyrial margin and on the outside by a more or less well defined suture line connecting the beak with a small socket in the outside, posterior face of the tooth. These narrow triangular spaces usually can be easily differentiated from the remainder of the interarea by the difference in color. In punctate shells the palintrope is punctate, but the dental area is impunctate. In a cross section of the palintrope the triangular area is also three-sided and is supported by the dental lamellæ.

The teeth of *Rhipidomella* vary from the usual type described above. They form the margin of the umbonal cavity and rest on the floor of the valve with little or no supporting plates, and project dorso-laterally as blunt points.

SOCKETS.—There are sockets in both valves which receive articulating processes from the opposite shell. In the ventral valve there are two kinds of sockets associated closely with the teeth: (1) Accessory dental sockets in the postero-lateral face of the teeth (see t. fig. 2); and (2) a crural fossette or crural socket⁶ on the inner face of the teeth.

1. The accessory socket in the tooth of the ventral valve is located in the postero-lateral surface of the tooth next to the hinge-line and on the outside margin. It articulates with a small



FIG. 2.—Diagram showing the ventral interarea of *Valcourea*, with accessory sockets in the teeth (*Acs*).

apophysis or tooth situated on the outside of the dental socket of the dorsal valve. This accessory articulation is common throughout the Orthoidea and in strophomenids, spiriferids, etc.

2. The crural fossette is a more or less deep groove, usually defined by an oblique ridge, located in the inner face of the tooth just ventrad of the delthyrial margin. Not uncommonly the fossette is not sunk deeply beneath the surface of the tooth but is made by a small subtriangular plane surface defined by an oblique ridge, a type frequently seen in the family Orthidæ. The function of the crural fossette is to articulate with the carinate, or, in some genera, expanded postero-ventral edge or face of the brachioaphore. In *Hesperorthis* the fossette is small, but the oblique ridge defining it is prominent. In the articulation of this shell each tooth fits into the socket which is located outside the brachioaphore; it extends into the socket a distance equal to the plane or sunken face of the crural fossette, while the oblique ridge rests on the posterior or postero-ventral edge of the brachioaphore. It follows then that the brachial apparatus of the orthid plays an important rôle in the articulation of the shell, a rôle no less important than that of the teeth and sockets.

The crural fossette of *Parmorthis* (pl. 21, fig. 10) is developed to a remarkable degree. It is an elongate, deep groove extending nearly to the floor of the valve and terminating in a deep socket. The oblique groove receives the postero-ventral edge of the crural base, and the socket at the end of the groove articulates with a slight expansion near its ventral extremity.

DENTAL PLATES.—Beneath each tooth there are as a rule two more or less strong plates dividing the space beneath the overhanging palintrope into three chambers, two lateral ones and a central one, the delthyrial cavity. These plates have been most commonly termed "dental lamellæ" or "dental plates." Thomas calls them "delthyrial supporting plates" and Fredericks speaks of them as "lamellæ apicales." We prefer to remain by the older terms "dental plates" or "dental lamellæ."

⁶ The term crural fossette ("fossette crurale") was used first by Kozłowski (Bib. Univ. Lib. Polonæ, A, 1927, fasc. 17, p. 8, fig. 1).

Thomas⁷ challenged the general conception that these plates gave support to the teeth. He says:

As to the function of these plates there appears to be greater reason for regarding them as supports of the areal portion of the pedicle valve than as dental supports. It is certain . . . that they are not in all cases directly connected with the teeth, while the connection in other instances need not necessarily imply the primary function of dental support. The delthyrium is situated at the weakest part of the areal portion and the plates are developed along its lateral margins and adjacent to the deltidium. This is just the position where one would expect a strengthening of the valve to take place. It seems preferable, therefore, to call such "dental" lamellæ the "delthyrial supporting-plates."

It has been the experience of the writers that in the Orthacea these lamellæ are invariably connected with the teeth. Thomas' argument that these plates support the palintrope at its weakest point is not conclusive, because there are many strophomenoid genera with long interareas that have no dental supports reaching the floor of the valve, and among the orthids the oldest known genus, *Nisusia*, is also without them. Furthermore, shells having broad overhanging palintropes, such as *Hesperorthis* and *Plectorthis*, are commonly provided with thin, delicate, short dental plates of the receding type, but shells with shorter palintropes and more ventricose valves have ponderous dental plates, e. g., *Orthis s. s.* and *Archæorthis*. Where these lamellæ are present, they undoubtedly serve the double function of supporting the teeth and the palintrope.

Dental plates may be described as *receding* when they extend as ridges under the teeth and the palintrope, and finally attain the floor of the valve near the apex only. Examples of this type are common in American orthids such as *Hesperorthis* and *Schizorammina*. The dental plates are called *advancing* when they slope forward and are continued around the lateral margins of the muscle field as more or less well defined ridges, as in *Schizophoria*. The term *obsolete* may be applied to dental plates when the lateral umbonal cavities have been so filled by adventitious testaceous matter as to obliterate them. This condition is common in old shells, so that the observer, if he does not take the precaution to examine interiors of young specimens of the same species, may fall into the error of describing the particular species or genus as possessing no dental plates. Such an error was made by Hall and Clarke⁸ in their definition of *Orthorhynchula*, which they say is without dental plates. The young of that genus, however, are provided with well developed receding dental lamellæ.

SPONDYLIUM

HISTORY OF THE TERM.—The term spondylium (from the Greek word for vertebra) was proposed by Hall and Clarke (1892) in their discussion of *Clitambonites*. They say of *Pronites adscendens* Pander:⁹

On the interior of the valve the dental lamellæ are very strongly developed, converging and uniting in the median line before reaching the bottom of the valve; thus forming a spondylium [a spoon-shaped plate], which with the deltidium encloses a conical subrostral vault . . . This term will apply with equal propriety to the similar plate existing in the pedicle-valve of other brachiopods, e. g. . . *Pentamerus*, *Camarella* [*Camarophoria*, etc.].

Later these authors add:¹⁰

It has become evident since the introduction of the term that these processes in the two valves [spondylium and cruralium of *Pentamerus*], though similar in aspect, are similar neither in origin nor function, and it becomes necessary to modify the application of this term. Hence it is proposed to restrict the term *spondylium* to the plate existing on the pedicle-valve, and to the plates of the brachial valve, whether united or discrete, the name *cruralium* will be applied.

The *spondylium* is an area of muscular implantation. In its early or incipient condition it is evident that it originates from the convergence and coalescence of the dental lamellæ, and forms a receptacle for the proximal portion of the pedicle, and for the . . . pedicle muscles. In *Clitambonites* and *Pentamerus*, where it attains its

⁷ Mem. Geol. Surv. Gt. Brit., Pal., vol. 1, pt. 2, 1910, pp. 100-101.

⁸ Pal. N. Y., vol. 8, pt. 2, 1893, p. 181.

⁹ Op. cit., pt. 1, p. 234.

¹⁰ Pt. 2, pp. 331-332, 335 footnote, 341.

greatest development, it bears all the muscles of the valve, the central adductor, and the lateral diductor scars being often clearly defined, while the posterior portion of the plate is still reserved for the attachment of the pedicle, if functional. In the pentameroids the median septum of the pedicle-valve supporting the spondylium, is formed in a similar manner by a continuation and coalescence of the dental plates, and wherever the median supporting septum exists in this group, it will probably be found to have this composition. Median and lateral septa, however, in the valves of the Brachiopoda, have a highly diverse origin in different cases. In most instances, except where bearing spondylia, they are evidently of muscular origin and surfaces of muscular attachment, as shown in *Spiriferina*.

[The spondylium is of early manifestation.] It appears in a highly developed state in conjunction with the unmodified deltidium [delthyrium], first in *Protorthis*, of the Cambrian, then in *Polytæchia*, *Syntrophia*, *Clitambonites* and *Scenidium*, of the early [Ordovician] and later Silurian and of the Devonian.

Schuchert¹¹ formerly held that the spondylium

probably had its origin in an excessive deposit of testaceous matter about the bases of the powerful adductors, diductors, and pedicle muscles. Growth of the individual necessitates the progressive anterior movement of the muscles, and when these are large there is but little or no space left between or outside of them for the viscera and genitalia, which are therefore crowded farther and farther anteriorly. This condition naturally produces constant pressure of the genitalia against the anterior base of the forming spondylium, and since pressure causes resorption or diverts testaceous deposition, it follows that these organs will gradually produce cavities for their relief beneath this plate.

This explanation certainly appears true for the platform in the atrematous Trimerellidæ, but it is now apparent that this is not the way the thin, plated, true spondylia of the Clitambonitidæ and Pentameridæ were made. It is clear that what Schuchert was describing is the origin of what is now called the sessile spondylium (spondylium discretum) so well developed in the Billingsellidæ.

Hall and Clarke give the correct function for the true spondylium when they say that it is "an area of muscular implantation," originating from the convergence and coalescence of the dental lamellæ, and uniting either with a median septum or with the floor of the shell, but their further statements about its making, in connection with the deltidium, a pedicle-sheath that had its first stimulus of growth in the prodeltidium is, as we now see, wrong. What Schuchert and the older students of brachiopods did not see is that the muscle-bearing platforms of the Trimerellidæ, the spondylia of *Clitambonites* and *Pentamerus*, and the cella of *Merista* are not homologous structures, since, as we now know, all are of independent origin, arising in different ways though functioning more or less alike. Sessile spondylia (spondylia discreta) are common in the Middle and Upper Cambrian, but true spondylia are not present until late in Cambrian time and are chiefly characteristic of the Ordovician and Silurian, while the cella type of muscle plate is of Middle and Upper Ordovician origin, appearing first in *Cyclospira* and *Dayia*.

What Schuchert in 1897 regarded as the primitive attached spondylium (= sessile spondylium), Walcott in 1912 called the pseudospondylium, and states that it occurs in *Nisusia*, "*Billingsella*," *Eoorthis*, *Finkelburgia* (free in front) and *Huenella* (free at the sides). The sessile or "pseudospondylium" of *Eoorthis*

appears in *Orthis* . . . of the Ordovician and later faunas, probably as a reversion from a free spondylium [here Walcott, as we now know, is clearly wrong]. On the line of descent to *Protorthis* the pseudospondylium becomes a free spondylium and continues on through *Syntrophia* and *Clarkella* into the Ordovician and Silurian Pentameridæ and Clitambonitidæ.¹²

Walcott asked Ulrich to comment on the kinds of spondylia, and this he did as follows.¹³ The term spondylium, he says,

applies only to the typical free or medially supported umbonal camera or spoon . . . and corresponds to a ventral muscular area which is raised above the floor of the valve and formed by the convergence and union of the dental plates . . . The manner in which the spondylium is attached to the bottom of the valve is so variable that the feature does not seem to be of more than generic consequence.

Ulrich then points out the great variability in a number of genera.

¹¹ Bull. 87, U. S. Geol. Surv., 1897, pp. 99-101.

¹² Walcott, 1912, p. 307.

¹³ In Walcott, 1912, p. 308.

Kozłowski¹⁴ has recently made a detailed study of the spondylium in the Pentameracea and has reached some striking conclusions. He has shown that there are two types of spondylia in the Pentameracea as constituted by Schuchert in 1913. One of these types, in which the spondylium is supported by a simple septum, he calls the "spondylium simplex," and thinks it originated from a pseudospondylium by lateral crowding of the ovarian bodies and consequent resorption of the deposit forming the base of the pseudospondylium. The Clitambonacea are characterized by this type of spondylium and Kozłowski finds this superfamily to be more closely related to the orthids than to *Pentamerus*. In his conclusion we concur, having arrived at the same opinion independently but using different criteria as well, namely, the pallial and ovarian impressions and the cardinalia.

Characteristic of the second group—the Pentameracea—is the "spondylium duplex." In this type the spondylium is elevated on a septum which is clearly composed of two parts thought to have been produced by the squeezing of the two dental plates together due to lateral pressure from the ovarian bodies. This type of spondylium is common to the pentamerids, but the cardinalia are much more characteristic than is a spondylium duplex which is known in *many* other genera.

PRESENT VIEWS AND DEFINITIONS.—We may add that the dental lamellæ and the floor of the valve between them are in many genera bound together by a chamber called the delthyrial cavity, and in most of the orthids the floor of this space is the seat of attachment of the various muscles. In other orthid genera the dental plates converge and unite with each other medially on the floor of the valve, or are supported by, and fused with, a median ridge before attaining the shell floor, forming an elevated spoon-shaped structure. It is to the latter type of muscle platform that the term spondylium is now restricted. In rare instances among the oldest brachiopods (*Protorthis*) the dental lamellæ unite to form a freely suspended spoon without the intervention of a median septum. These various types of muscle platforms may be briefly defined as follows:

1. **DISCRETE SPONDYLIIUM.**—This, Kozłowski's spondylium discretum, designates the condition in which the dental lamellæ converge but slightly and extend directly to the floor of the valve, but never become united. This type of muscle cavity occurs in *Porambonites*, *Huenella*, and a host of other orthid shells. It is not a spondylium, but the structure does suggest how the genuine spondylia arose, namely, by the complete convergence and union of the dental plates above the floor of the valve, and their support by a median septum standing on the floor of the shell.

2. **PSEUDOSPONDYLIIUM.**—This term was introduced by Walcott¹⁵ for "the rudimentary spondylia attached directly to the inner surface of the valve, as in *Billingsella*." In all the species listed under the genus *Billingsella* in the present work the dental lamellæ do not converge but extend vertically to the floor of the valve and conform in all essentials to the type of muscle platform called by Kozłowski the spondylium discretum. In some species, however, the anterior portion of the muscular area is elevated on a callosity. This shell thickening within the delthyrial cavity and its connection with the dental lamellæ make it appear that these plates are united but in reality they are discrete, resting on the floor of the valve. It is to this type of muscle platform that we propose to limit the term pseudospondylium.

Pseudospondylia are excellently exhibited in *Glossorthis* (see pl. 4, figs. 9, 12), *Linoporella* (see pl. 18, figs. 13, 14, 18), and *Finkelburgia* (see pl. 13, figs. 6, 11). In these genera the callus beneath the muscle attachments is extended from the floor to the inside face of the dental lamellæ. Anteriorly the callus is thick and in *Finkelburgia* is extended forward as a low ridge. Specimens of *Linoporella* kindly loaned by Dr. A. H. Westergaard of Stockholm show a complete series from the young stage with discrete dental lamellæ and unthickened muscle attachments to a condition in which a typical pseudospondylium with a median ridge has been developed. This series is illustrated on plate 18.

Pseudospondylia are naturally more developed in old or late mature shells, as young individuals do not deposit much callus. Since, therefore, the pseudospondylium is a feature of mature shells only, it is obvious that it has a minor value in the taxonomy of the Brachiopoda.

¹⁴ Pal. Polonica, 1919, pp. 122-125.

¹⁵ Camb. Brach., 1912, p. 295.

3. SPONDYLOID.—This term is suggested for a structure simulating a spondylium in form but produced by the deposition of adventitious testaceous substance on and about the dental lamellæ, swelling them laterally until union is effected. This type of structure is well exhibited in *Porambonites*. In late mature or gerontic individuals of this genus, adventitious shell has been deposited on the dental lamellæ and on the floor of the valve in front of them, and may be produced forward sufficiently to simulate a median ridge or septum. In old shells this structure so closely resembles the spondylium in pentamerids that Noetling and subsequent workers have been misled into the conception that the thickening of the dental plates in *Porambonites* is a spondylium.

4. FREE SPONDYLIUM.—Here the dental plates converge and unite to form a spoonlike muscle platform that hangs suspended in the ventral valve, since it is not supported by a median septum as in the typical forms of spondylia. This type is exceedingly rare, being known in *Protorthis* of the Middle Cambrian, and the younger genera *Holorhynchus* and *Cymbidium*.

5. SPONDYLIUM OR SPONDYLIUM SIMPLEX.—The term spondylium has customarily been applied to the spoon-shaped muscle platform formed by the convergence and union of the dental lamellæ with a median septum, regardless of the structure of the septum. Kozłowski,¹⁶ however, has shown that the spondylia are differently constructed and are therefore polyphyletic in origin, and has consequently defined several kinds. He shows that the spondylium in *Skenidium* and *Clitambonites* is different in origin from that in the Pentameracea. In *Clitambonites* the spondylium is formed by the union of the dental plates with a simple median septum (euseptum), the whole forming one piece. To this type of spondylium he gave the name spondylium simplex. As this is the simplest type of supported spondylium, we may call it spondylium and drop the limiting word simplex.

The spondylium is one of the characteristics of the subfamily Clitambonitidæ and is seen also in the Syntrophiidæ and Skenidiidæ.

6. DUPLEX SPONDYLIUM.—The above type of spondylium is in decided contrast to that in the Pentameracea (*Conchidium*), in which the supporting septum is actually double and composed of two united vertical plates. To the latter type Kozłowski has applied the name spondylium duplex, and it appears not to occur in any genus of the Orthoidea,¹⁷ but is characteristic of the pentamerids, where it is associated with a definite kind of crural apparatus.

In its evolution, Kozłowski believes that the spondylium simplex has arisen from the pseudo-spondylium. The genital organs are thought to have resorbed the testaceous deposit about the base of the dental plates and under the muscle attachments. The resorption has gone so far as to leave a rather narrow septum underneath the seat of muscle attachments. This is, in its essentials, precisely the same idea held by Schuchert in 1897.¹⁸ The spondylium duplex, however, is considered by Kozłowski to have originated in a different manner, i. e., through lateral crowding by the sexual glands, which has pushed the dental lamellæ gradually together.

SEPTA

Vertical septa are usually not conspicuous features of the ventral interior, but in some genera rather prominent ridges or septa are developed in connection with the musculature, deltidium, and pedicle attachment. Such ridges usually have value in species making but only rarely have they generic significance.

In shells wherein a pedicle callist or a deltidium is present, it is not uncommon for a small septum to extend forward from the callist or deltidium for a short distance, dividing the back ends of the diductor scars. This ridge is commonly formed in old shells and is the result of deposition of adventitious shell between the muscles. Such septa are, however, of little taxonomic significance.

¹⁶ 1929, pp. 122-126.

¹⁷ The writers have not seen a thin section of the spondylium of *Enteletella* and its detailed nature can not be determined from Likarev's figure.

¹⁸ Op. cit., pp. 99-100.

In shells having a spondylium there may be other septa in addition to the median one. This is true notably of *Gonambonites*, *Clarkella*, and *Yangtzeella*, in which the lateral septa probably play a secondary part in the support of the spondylium. In *Clarkella* the several lateral accessory septa appear to be excessively developed ovarian ridges, and such are common among the syntrophiids and orthids.

A few genera that have greatly developed diductor scars, especially where these wrap about and enclose the adductor scars, as in *Rhipidomella*, may develop short, low septa in front of the latter impressions; the septa then separate the antero-median extremities of the diductor scars. These septa are also of no special taxonomic value.

A few genera are provided with a broad and low median ridge which, besides dividing the diductor impressions, also bears the adductor muscles. This type of septal ridge is seen best in the Schizophoriidæ, in which its development can be traced from a low ridge in *Pionodema* and the early Schizophorias to a high septum in *Orthorichia* and *Enteleles*. The same kind of median septum is also seen in certain stocks of the dalmanellids such as *Cariniferella*, and in these the ridges likewise bear the adductor muscles.

There is an interesting development of a median ventral septum in *Parenteleles*. Here the dental plates are similar to those of *Enteleles*, but are more widely divergent. The median septum, however, has its origin a short distance anterior to the apex, continuing forward and increasing in height in the same direction. But at the anterior end of the septum, just at the point of origin of the shell fold (ventral), there is a small inverted V-shaped chamber, here termed the *cella*;¹⁹ this chamber evidently acts as an arch to support the dorsal septum above the inner sulcus produced by the external fold. The septum in this genus is further distinguished from that of *Enteleles* by its expanded, rounded dorsal edge.

MUSCULATURE

By means of muscles, brachiopods are enabled to open and close their valves, and to a limited extent to protrude and retract the pedicle and to adjust the position of the shell. In the articulates there are three sets of muscles: the *diductors*, which by contraction open the valves; the *adductors*, which by contraction close the valves; and the *pedicle muscles* (including the adjustors), which by contraction "serve to alter or adjust the position of the animal as a whole by turning it in various directions."²⁰ All of the muscles traverse the visceral area. The attachment of the muscles to the valves leaves as a rule well marked scars. The diductor muscles which attach to the cardinal process are distinguished as the principal or *anterior diductors*, while the much smaller pair are the accessory or *posterior diductors*; the latter are seen in the ventral valve as two small scars posterior to the adductors. In most fossil brachiopods it is only the anterior diductor and the adductor scars that are impressed.

According to Thomson,²¹

The pedicle-muscles serve partly to attach the pedicle to the shell, and partly to retract the pedicle or to allow the shell to erect itself. They consist of an unpaired muscle [unknown as such in orthids, where they are always paired] running from the ventral side of the pedicle to the ventral valve, where it determines a transversely elongated scar lying posteriorly of the other scars, and, in addition, two pairs known as the dorsal and ventral adjustors. The dorsal adjustors are attached to the hinge-plates or other similar structures in the dorsal valve . . . , while the ventral adjustors form two scars in the ventral valve lying outside the adductor-scars. The pedicle-muscles, not being relatively very strong, do not form strong scars, the median unpaired muscle making the strongest.

In the Orthacea the ventral muscle field begins small, and progressively expands in later forms. Hall and Clarke saw this long ago, saying:²²

The entire muscular system on the ventral side of the body, is, in primitive forms, inserted upon the base of the pedicle [delthyrial] -cavity. This is apparent from a study of such a shell as *Orthis callactis*, where it is perfectly clear that no muscular bands were attached to the pedicle-valve outside the limits of this strong and con-

¹⁹ From the Latin word for small or extra room.

²⁰ Parker and Haswell, Text-book of Zoology, vol. 1, 1921, p. 358.

²¹ Brach. Morph., 1927, p. 30.

²² Pal. N. Y., vol. 8, pt. 2, 1894, p. 338.

densed posterior area, which is but a sessile spondylium. [In some shells] the original contents of the pedicle-cavity may be represented by enormous muscles whose scars extend almost to the anterior margin of the valve, as in *Hipparionyx* and *Rhipidomella*.

The detail of the muscle-scars in brachiopods is usually difficult to determine, because of the poor preservation of the inner surface, or because of the thinness of the shells. Furthermore, as the animals grow larger, the muscles migrate forward, leaving more or less elongate tracks widening toward the front. On the other hand, the tracks do not always afford the detail of the muscles because the mantle later on covers up the posterior portions of the tracks as migration continues. It is therefore not uncommon that a doubt may be entertained as to what the actual marks represent in detail. To cover these various aspects of the muscle-scars we deem it best to adopt the following terms from Buckman:²³

1. "*Muscle-mark*—any mark indicating muscular attachment.
2. "*Muscle-track*—the course down the valve shown by successive muscular attachments.
3. "*Muscle-scar*—more or less defined areas representing the ultimate muscular attachment."

In general, when the preservation is favorable, four sets of muscle impressions may be distinguished in the ventral valve, as follows: (1) the principal or anterior diductors, (2) the adductors, (3) the adjustors, (4) the accessory or posterior diductors. Of these four sets, the first three are usually visible, but the accessory diductor scars are rarely to be seen, and in some instances the adjustors are not determinable.

(1) ANTERIOR DIDUCTOR MUSCLES.—The diductor impressions are always the largest scars in the ventral valve. In the early impunctate genera, their tracks and scars are usually rather narrow and straight, and never enclose the adductor impressions at the front. In later genera, such as *Dinorthis s. s.*, *Dinorthis (Plæsiomys)*, and *Rhipidomella*, the diductor scars enclose the adductors.

(2) ADDUCTOR MUSCLES.—When the actual adductor scars are visible they are usually hemi-elliptical in outline and separated by a low ridge which may be single or double. In some genera the adductor impressions can not be determined, but their position is marked by a linear track. In a few genera, such as *Platystrophia*, *Mcewanella*, and *Productorthis*, there is no trace whatever of either the scars of attachment or the tracks. In other genera (*Schizophoria*, *Orthotichia*, and the *Enteletinæ*), the adductor muscles were borne on a high vertical septum, consequently their marks are not recorded on the shell.

(3) ADJUSTOR OR PEDICLE MUSCLES.—These muscles are not always clearly defined on the valves and have not been determined in all genera of the Orthoidea. The position of these muscles, however, is always outside of, and posterior to, the diductors at the base of the dental lamellæ, or they are more or less elevated on the side of these plates. As would be expected from their position, these muscle impressions are usually elongate, and rarely present the semi-flabellate outline commonly seen in the diductor scars. The adjustor scars are the most variable of the muscle markings and in this work little reliance has been placed on them in the establishment of genera. Where good material is available, however, they may be of some use in the making of species.

In their great work on brachiopod genera, Hall and Clarke²⁴ have applied two terms to the set of muscles we are calling adjustors. In the text of the discussion of *Dinorthis* they refer to these muscles as "adjustors," but in the legend to Plate V, where this genus is figured, they call them "posterior diductor muscles." We prefer to use the term adjustor muscles because these scars have precisely the same position in reference to the diductors as in Recent genera. Furthermore, the posterior diductor scars in living forms are located just posterior to the adductor impressions. Similarly situated scars can occasionally be seen in Paleozoic shells and their presence lends support to our usage of the term adjustor. It must be admitted that similarity of position does not prove homology of the muscle-scars in question, but in the absence of more definite knowledge of the soft parts of these Paleozoic shells, we can only compare the structures in the older genera with those in the Recent forms.

²³ Brach. Namyau beds, 1917 (1918), p. 90.

²⁴ Pal. N. Y., vol. 8, pt. I, p. 195.

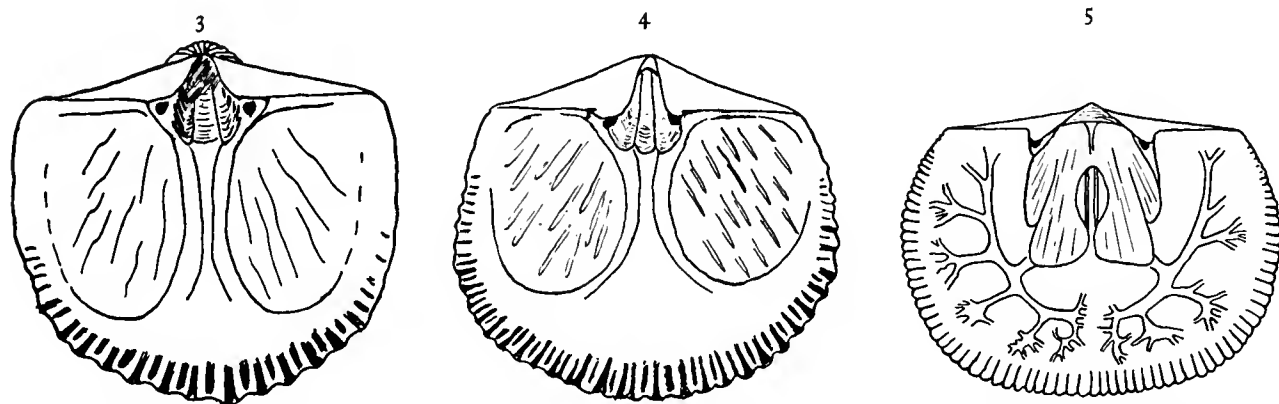
(4) ACCESSORY DIDUCTOR MUSCLES.—In *Laqueus* and other terebratulid genera there is an accessory diductor set located immediately posterior to the adductor scars. From the presence of such marks in these recent shells it might be suspected that homologous muscle patches should occupy a similar position in the orthids. Such scars have been described by Sardeson²⁵ in *Dalmanella emacerata*, in which they are located just posterior to the adductors and between them and the pedicle callist, hence in precisely the same position as in *Laqueus*. In shells like *Dinorthis subquadrata* and *Rhipidomella* there may be a corresponding set of muscles associated with the adductors, although these were not clearly seen by us.

According to our interpretation of this set of muscles as adjustors, there can be no corresponding set of scars on the dorsal valve, since these muscles are here attached to the pedicle.

PALLIAL AND GENITAL MARKINGS

The mantle (or certain of its layers) is folded upon itself at various points, enclosing cavities, or *pallial sinuses*, which contain the body fluids and frequently portions of the genital organs.

PALLIAL MARKINGS.—The markings of the main pallial trunks are often seen in the Cambrian



FIGS. 3-5.—Ventral pallial and ovarian markings. 3, *Orthis s. s.*; this type characterizes the family Orthidae as here described. 4, *Schizoramma*, in which the markings are essentially the same as in *Orthis* and *Hesperorthis*. 5, *Dinorthis (Plasiomys) subquadrata* (Hall); notice here that the main trunks extend from the anterior of the diductor scars. In the ventral valve the pallial trunks in all orthoid brachiopods begin at the same place.

genera of Atremata (*Obolus*, *Lingulobolus*, *Lingulella*, *Bicia*, *Dicellomus*) and of Neotremata (*Obol-ella*, *Acrothele*, *Botsfordia*, *Acrotreta*). Accordingly these markings should be common among the Cambrian Orthacea, and so they are. They are especially well seen in *Billingsella*.

In living brachiopods, according to Thomson,²⁶

The pallial sinuses take the form of great trunks, entering the mantle-lobes from the cœlome, and generally branching repeatedly towards the margins. The disposition of the sinuses varies considerably in different groups, and it is probable that these characters have at least superfamily value in classification.

The pallial marks have been found of great use in defining some of our families.

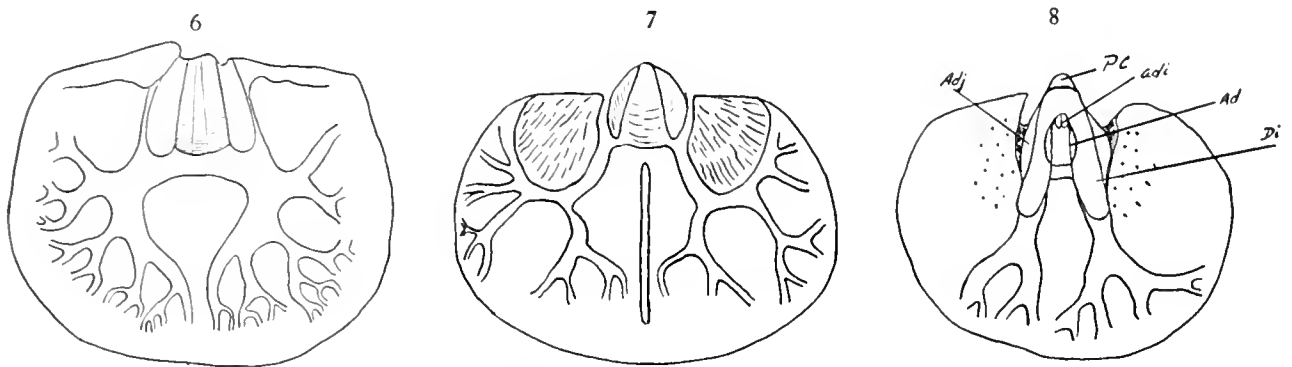
In general, the pallial markings of the ventral valve are rather simple as regards the main trunks. Their general arrangement is foreshadowed in the Cambrian genera of the Billingsellidae in the two prominent trunks which radiate antero-laterally from the forward ends of the diductor scars, thence splitting and diverging toward the front and sides of the valve. One of the anterior branches of each trunk swings dorsally and runs nearly parallel to the lateral margin. The other, shorter branches extend inward and may or may not unite near the mid-line of the valve (see pl. 1, fig. 10).

²⁵ Amer. Geol., vol. 19, 1897, p. 93.

²⁶ Brach. Morph., 1927, p. 11.

In the Orthidæ and Clitambonitidæ the two main trunks are clearly visible but instead of being widely divergent as in the Billingsellidæ they extend forward near the mid-line of the shell, being separated by a narrow septum only (t. figs. 3, 4; pl. 2, fig. 18; pl. 6, figs. 18, 26; pl. 8, fig. 10). At the front they may or may not diverge. In the higher families of the Orthoidea such as the Dinorthidæ and Plectorthidæ the pallial markings are more complicated but of the same fundamental pattern. In *Plæsiomys* (see t. fig. 5; pl. 10, fig. 26) the main trunks are short and rather narrow, diverging from the antero-lateral extremities of the diductor scars. The main trunks branch almost immediately after their inception, sending one trunk posteriorly and another antero-medially. Each of these subsidiary trunks gives rise to minor branches toward the front and sides of the shell. In *Mimella* (see t. fig. 6; pl. 12, fig. 20) the general arrangement of the trunks is on the plan of *Dinorthis*, but details of the branching are different. *Orthostrophia* (t. fig. 7) has the two divergent trunks of the Dinorthidæ which branch into subsidiary trunks, but in addition has one or two minor trunks extending forward from the adductor tracks. These may actually be branches from the main trunks in front of the diductor impressions, but no lines of contact were observed.

In the Dalmanellidæ the two main trunks are visible in many of the genera, extending forward from the diductor impressions. The branching of the main trunks into subsidiary rami is more or less complicated (t. fig. 8; pl. 17, fig. 22).



FIGS. 6-8.—Ventral pallial markings. 6, *Mimella melonica* (Willard). 7, *Orthostrophia* aff. *O. strophomenoides* (Hall), in which they are of the same type as those of *Dinorthis* and *Mimella*. 8, *Dalmanella ignota* Sardeson: Pc, pedicle callist; adi, accessory diductor scars; Adj, adjustor scars; Ad, adductor scars; Di, diductor scars.

GENITAL OR OVARIAN MARKINGS.—In living brachiopods the genital glands (brachiopods are dioecious) are, according to Thomson,²⁷

rather thick, convoluted bands . . . varying somewhat in size . . . There are four glands in each animal, two on the ventral and two on the dorsal side . . . The glands in some genera are bound down to the shell by muscular ties, which give the shell a pitted appearance, the so-called ovarian impressions.

These markings are usually dissimilar on either valve, and in some Orthacea are not observable at all.

Genital or ovarian markings consist usually of more or less reniform areas in the umbo-lateral portions of the valve bounded by the main trunks or the postero-lateral branches of the pallial sinuses. Within the reniform areas are elevated ridges radiating from the umbonal cavities. These probably represent attachments of the ovarian bodies. Reniform ovarian areas are most prominent in the Orthidæ and Clitambonitidæ, but in many genera these markings are not represented by reniform areas but by wavy ridges or by pustules that are aggregated in the umbo-lateral spaces.

²⁷ Brach. Morph., 1927, p. 13.

MORPHOLOGY OF THE DORSAL INTERIOR

NOTOTHYRIAL PLATFORM

The interarea of the dorsal valve in most genera of the Orthoidea is centrally cleft by a triangular opening called the notothyrium, which lies opposite the delthyrium of the ventral valve; both have been described in a previous section of this memoir. Beneath the margins of the notothyrium is a cavity, the notothyrial cavity, which is deep or shallow depending on the degree to which the floor has been built up by deposition of shell substance. The floor of this cavity is commonly built ventrally from the floor of the valve by the accretion of testaceous substance, producing a swelling within the walls of the cavity. To this swelling the term "platform" has recently been applied²⁸ but that term has already been used for the elevated muscular platform of the Trimerellidæ (see p. 9). To avoid using this term for two very different structures we here suggest the designation *notothyrial platform*.

DENTICLES AND SOCKETS

DENTICLES.—Teeth for the main articulation of the valves occur only in the ventral shell, but accessory processes fitting into the sockets in the posterior face of the teeth of the ventral valve occur in most of the genera. These are here called denticles. They are usually wider than long and are located on the outside wall of the socket. This accessory apparatus makes for rigidity in articulation (t. fig. 2).

SOCKETS.—The socket which receives the tooth of the ventral valve in articulation is always located between the inner shell wall and the outer face of the brachiophore. The simplest type of socket occurs in the Billingsellidæ, Orthidæ, and Dalmanellidæ, in which it is merely the cavity between the brachiophores and the inner wall of the valve. This may or may not be slightly excavated beneath the palintrope, or into adventitious shell matter laid on the wall of the valve.

A second type of socket is that which is found in the Plectorthidæ, Wattsellidæ, and Schizophoriidæ. In these families the socket is defined by a small concave plate (fulcral plate) joining the brachiophore to the wall of the valve (see pl. 22, fig. 25).

CARDINALIA

The articulating apparatus, the brachial supports, and the cardinal process are together known as the *cardinalia*. Until recently this structural ensemble has been little used in the construction of genera and families. Hall and Clarke in their study of *Orthis* gave little attention to the brachial supports and cardinal process, and accordingly did not see the significant differences between *Hebertella*, *Dinorthis*, *Orthis*, *Plectorthis*, and *Dalmanella*, differences pointed out in the present work. The cardinalia are intimately bound up with the brachia and the musculature of the brachiopod and consequently are important structures.

CARDINAL PROCESS

Nothing in the nature of a cardinal process is ever seen in the inarticulate orders Atremata and Neotremata. Such first appears among the Orthacea of the Cambrian, but at no time in this period can it be said to be strongly developed, and even in certain of the primitive genera it is a linear ridge that may be absent in some species of the same genus. In *Kutorgina* no cardinal process is known, and one may be present or absent in *Nisusia* and *Jamesella*. In the late Cambrian a cardinal process is of sporadic occurrence in nearly all of the genera.²⁹

The cardinal process is located on the notothyrial platform in the mid-line of the shell. It may be a simple, linear, more or less thickened ridge, or it may be a far more complex structure and then

²⁸ Bancroft, B. B., Mem. and Proc. Manchester Lit. and Philos. Soc., vol. 72, 1928, p. 175.

²⁹ Walcott, Camb. Brach., 1912, p. 306.

divisible into two parts: (1) the *shaft* or anterior element, and (2) the *myophore* or posterior part, the seat of attachment of the diductor muscles. The shaft is usually extended forward for some distance or may merge with a median ridge. Rarely is the shaft much abbreviated (*Rhipidomella*). The head or myophore may be expanded, multilobate, and crenulated, or it may be compressed laterally so that the actual muscular attachment takes place at the thinned posterior extremity of the process (see pl. 17, fig. 26). In some of the later genera, such as *Schizophoria*, the process, which in young shells has much the same form as in *Rhipidomella*,

becomes absorbed and thus narrowed with age making a thin and sharp ridge; concomitant with this change is the formation, in the delthyrial [notothyrial] cavity, of one, two or even three minor ridges on each side of the original process, so that in old shells the posterior face of the process appears to be multilobate.³⁰

Accessory ridges are also present in some species of *Schizorammina* (see pl. 5, fig. 14).

The following nine types of cardinal process have been observed in the Orthacea:

(1) The *Orthis* type, which consists of a thin ridge situated in the middle of the notothyrial platform and usually extending its whole length. This ridge is generally thicker at its base; it may or may not be expanded toward the front. Scars of muscular attachment may actually be

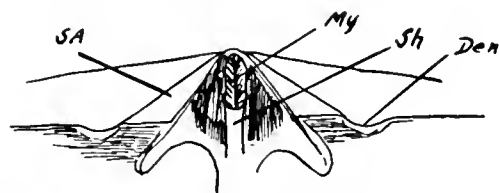


FIG. 9.—Diagram showing features of the cardinalia. *My*, myophore of the cardinal process; *sh*, shaft of same; *Den*, denticle on outside wall of socket, which articulates with accessory socket in ventral tooth; *SA*, so called secondary area.

observed in some genera on the ridge, but they do not appear to be restricted to it, since in some species (see pls. 2 and 5) distinct muscle marks can be observed on the notothyrial platform at the base of the process. The development of a vertical ridge naturally increases the area of muscle attachment and so strengthens the pulling power of the diductor muscles. The *Orthis* type of cardinal process is the most primitive structurally and the earliest chronologically. Its first appearance is in the Middle Cambrian and it characterizes the Billingsellidæ, Orthidæ, and Clitambonitidæ. So far as our knowledge goes, this type of cardinal process is absent in punctate Orthoidea. A few punctate genera (*Harknessellina*, *Heterorthina*) have a cardinal process that simulates the *Orthis* type, but in all examples it can be shown to be a modified lobate or *Dalmanella* type.

(2) The *Productorthis* type (see pl. 3, fig. 11; pl. 4, fig. 15), a unique and very unusual variation from the ordinary kinds seen in the Orthoidea, which has been developed as an adaptation to the productoid form of the shell. The dorsal valve is nearly flat and the cardinal process rises abruptly from a posterior thickening of the shell and is directed posteriorly, extending for some distance beyond the margin of the hinge-line. The shaft is strong and thick, the myophore a compressed region on the postero-dorsal face of the shaft, clearly showing the diductor scars.

(3) The *Dinorthis* type (see pl. 9, figs. 3, 20), characteristic of the Dinorthidæ, in which the shaft is short and stout. In mature shells having this type of cardinal process, the median ridge appears not to be a continuation of the shaft of the process but is given off rather from the anterior end of the notothyrial platform. The shaft is subelliptical or suboval in section. In young mature shells the myophore is likewise oval or elliptical in plan, usually dilated slightly laterally, and clearly divisible into a right and left half by a more or less elevated ridge (*Plæsiomys*) or depression (*Dinorthis*) running along the long axis of the ellipse. Each half ellipse is strongly wrinkled by arcuate ridges running backwards to the margin of the myophore.

In shells having this type of cardinal process, age modifications introduce notable changes in size and shape. In *Plæsiomys* the shaft may be totally obliterated by enlargement of the notothyrial

³⁰ Hall and Clarke, Pal. N. Y., vol. 8, pt. I, p. 212.

platform as successive depositions of adventitious substance are laid upon it. The plan of the myophore may become distinctly oval or even subcircular, the central ridge becoming more elevated especially at the antero-ventral extremity. Such modifications result in a cardinal process not unlike that found in some of the *Dalmanellidæ*. In *Dinorthis*, wherein the two crenulated halves are divided by a depression, the ventral portion of the cardinal process may become distinctly bilobed, the lobation being produced by posterior growth of the cardinal process through the gradual enlargement of the lobes with increasing age. The slight depression dividing the crenulated halves of the myophore is not obliterated during growth.

(4) The *Hebertella* type, which is not unlike the preceding in its initial stages, having a short shaft confined within the notothyrial cavity and having the muscle attachment on its dorsal extremity. It differs, however, in having the myophore in late stages impressed into the sides of the shaft. In very youthful forms the muscles may be borne on the dorsal surface of the shaft as in the *Dinorthidæ*, but with increasing age the muscle attachments are sunk below the surface of the sides of the shaft. In old forms the myophore may appear as a rather slender septum crenulated on its sides and mounting a more or less stout shaft. In gerontic forms the muscle attachments may be sunk into the shaft at the dorsal portion of the cardinal process, but the ventral portion may be expanded and bulbous. This type has been observed in *Plectorthis*, *Doleroides*, and other members of the *Plectorthidæ* (see pl. 11, figs. 4, 17, 23, 26). It has not, however, been definitely noted in *Platystrophia*, in which the cardinal process is not uncommonly considerably resorbed and in some instances reduced to a mere remnant.

(5) The *Dalmanella* type, common to many endopunctate shells. Primitively the cardinal process has a short shaft and a distinctly lobate myophore. The latter may be either bilobate as in *Heterorthina* (pl. 17, fig. 32) or trilobate. The cardinal process of these shells is distinctly progressive, since all the diductor attachments are on the myophore. Usually there are clearly visible four distinct scars, but it is not uncommon for the middle two to be coalesced and in some instances elevated above (in a posterior direction) the outer two, and in that event the myophore is distinctly trilobate. In other forms the inner and outer set are combined, making a bilobed myophore. This bilobation may be expressed in the shaft, and with progressive posterior growth of the myophore there is left anteriorly a depression or cleft in the shaft (see pl. 17, fig. 32). As far as our researches have gone, these variations of the posterior portion of the cardinal process have no generic value, nor are they always constant in the same species.

Old-age thickening of the cardinalia, and of the cardinal process in particular, produces riotous growths. Such are seen commonly in *Dalmanella meeki* and another type occurs in *Levenea subcarinata* and *Isorthis perelegans*. In *D. meeki* and other dalmanellids the myophore may become so enlarged as to fill the notothyrium completely. In *Levenea* and *Isorthis* the anterior portion of the ventral lobe of the myophore may be produced forward along the shaft as a distinct process, giving to the whole structure the appearance of a fly's head with "tongue" or proboscis protruded.

There are several modifications of the *Dalmanella* type of cardinal process which should be mentioned, since they are distinct enough to mark groups of shells. These are:

(6) The *Rhipidomella* type, in which the shaft has its greatest extension in a ventral direction (at right angles to the plane of the commissure) and is scarcely developed anteriorly. The myophore is commonly large. The greatest development of this type of cardinal process is found in *Platystrophia planoconvexa*, in which it is remarkably robust (see pl. 19, fig. 24).

(7) The *Parmorthis visbyensis* type, in which the myophore is like that of *Dalmanella* but has been revolved 90° so that it is parallel to the plane of the commissure and is distinctly visible in dorsal view. The shaft is essentially obsolete, as the brachiophore plates and the cardinal process have become fused. This modification is no doubt developed to allow a greater pull of the muscles on the myophore (see pl. 21, fig. 8).

(8) The *Heterorthis* type (pl. 20, fig. 20), in which the median lobe of the myophore is elongated posteriorly at the expense of the lateral lobes, producing thereby a carinate ridgelike structure on the cardinal process. In molds of the interior this type appears to be a simple ridgelike cardinal process, but in well preserved specimens the primitive lobation is apparent.

(9) The *Pionodema* or *Schizophoria* type, in which the shaft is delicate, the myophore may or may not be lobate in front, while the muscle attachment is near the dorsal portion of the myophore, leaving an unoccupied portion ventrally. Here the muscle attachments are not uncommonly deeply sunk so that the myophore simulates the *Hebertella* type. Finally, in *Schizophoria* the cardinal process may be resorbed and its place occupied by low ridges (pl. A, fig. 14).

BRACHIOPHORES OR BRACHIAL APPARATUS

In previous works treating of the Protremata, little attention has been paid to the calcified brachial apparatus, and in consequence the classificatory value of these structures has been almost completely overlooked. In the present studies we produce some new knowledge regarding these parts in the most primitive families of the Protremata, and have used these structures, in combination with the other parts of the shells, to prove relationships of genera hitherto unsuspected. To facilitate more detailed description, it is necessary to have a new terminology defining the various parts of the cardinalia.

The simple brachial apparatus of the orthids has usually been termed the crura, but it is not yet established that these processes are homologous with the crura of the rhynchonellids or the "crura" of the terebratulids and spirifers, which continue unbroken into the descending lamellæ of the loops or spires. In the usual Paleozoic rhynchonellid, the crura are long curved processes borne on the inside of a socket plate or crural base. In the orthids, on the other hand, the structures commonly termed the crura are also the "socket plates," since they bound the sockets. Furthermore, these so called crura in many of the orthids actually have elongate processes which extend into the valve precisely as do the crura of rhynchonellids. In separated valves these processes are commonly broken off as is also the case among the rhynchonellids, but in a few orthids the entire brachial apparatus has been preserved (see pl. 5, fig. 24).

Among the orthids, we propose to apply the term *brachiophore* to the structures on either side of the notothyrium which bound the sockets and to which were attached the elongate *brachiophore processes*; to the latter in turn was fastened the lophophore. In some genera the brachiophores are supported dorsally by plates, and to these the name *brachiophore plates* or *supports* is given. It will be seen from the above that the brachiophore or so called crus of the orthid is evidently homologous with the crural base or socket plate of the rhynchonellid, rather than with the crus of the latter. Our terms are applicable only to the more primitive or orthoid stage of development of the brachia, and among these shells there are several types of brachiophores as follows:

(1) *Eoorthis-Billingsella* type (see pl. 1, figs. 19, 25).—Since the brachiophore in these forms is derived from that of the most primitive of the Cambrian orthids, it naturally should be of the simplest type. The brachiophore is a flat blade with its inner margin flush with the margin of the notothyrium and lying obliquely under its anterior surface. The dorsal palintrope thus overlaps the posterior or outer surface of the brachiophore. The socket is the space between the sloping outer face of the brachiophore and the palintrope. In the Billingsellidæ, Nisusiidæ, and Protorthidæ the sockets are narrow and slitlike, and the brachiophore is supported along its anterior surface by the swelling of the notothyrial platform (pseudocruralium of Walcott) which extends laterally under the anterior surface of the brachiophore. This type of brachial process may have evolved into the one seen in the Orthidæ (Orthinæ, Hesperorthinæ), Dinorthidæ, and Clitambonitidæ.

(2) *Orthis-Hesperorthis* type (see pl. 2, fig. 10; pl. 4, fig. 21; pl. 5, fig. 24).—This type is not unlike the previous one but is more advanced. The brachiophores were more efficient, since they had a greater antero-ventral extension. In this type the brachiophore is an elongate blade or rod, occasionally grooved along the inner face as in *Hesperorthis*, unsupported except for the addition of shell substance under the anterior face during the growth of the notothyrial platform. The brachial processes of the Russian *Orthis callactis-calligramma* group are very close to those of *Billingsella* and *Eoorthis* in their simplicity. On the other hand, the brachiophores of *Hesperorthis* are advanced, being grooved along the inner face and in well preserved shells terminated by an elongate process or point. The *Orthis* type of brachiophore is present in several genera in various modifications brought about by deposition of adventitious material. This is best seen in *Glyptorthis*, in which the notothyrial platform simulates that in *Hebertella*.

(3) *Clitambonites* type (see pl. A, fig. 7; pl. 8, fig. 6; t. fig. 10).—Here the brachiophores are simple blades or flattened rods, but are supported in a unique manner. Shell matter of the notothyrial platform is built up conspicuously under the cardinal process and is extended laterally for a considerable distance, forming, with the prominent median ridge and chilidium, an anchor-shaped structure. However, the original or youthful brachiophore is in some specimens clearly distinguishable from the adventitious shell matter. This type of brachial apparatus occurs in *Clitambonites*, *Vellamo*, *Gonambonites*, *Estlandia*, *Hemipronites*, *Deltatrete*, and *Pomatotrema*; also in certain shells referred to the Plectambonitidæ, as *Plectambonites* s. s., *Plectella*, and *Ingria*.

Another modification of the clitambonitid type is visible in *Productorthis*, in which the brachiophores are at first of the primitive flat blade type, but in later growth adventitious shell is laid down inside and outside of them and likewise around the distal end of the blade, forming cuplike structures. This type, in a somewhat modified form, also occurs in certain dalmanellids, totally obscuring the original brachial apparatus (see pl. 4, fig. 15).

(4) *Plectorthis-Hebertella* type (see pl. 11, figs. 4, 26).—Here the brachiophores are supported by concave plates which unite with the floor of the valve on each side of or beneath the

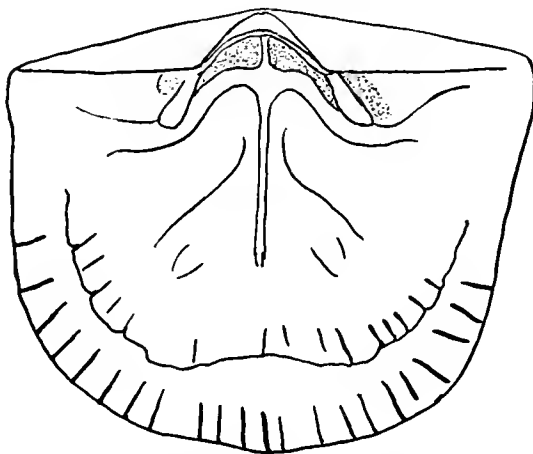


FIG. 10.—*Estlandia marginata* (Pahlen). Diagram showing brachiophores in place supported by a lateral swelling of adventitious substance.

cardinal process. The socket is defined, not by the outer face of the brachiophore, but by a small concave plate called the *fulcral plate*,³¹ located between the outer face of the brachiophore and the wall of the valve. This type of brachial apparatus characterizes the Plectorthidæ and *Finkelburgia* (see pl. 13, fig. 16). It is foreshadowed by *Orusia* (which is very close to *Finkelburgia*) in which the brachiophores are supported by subparallel plates. In young *Plectorthis* the brachiophore plates are commonly discrete but in older forms they unite beneath the cardinal process or with a median septum.

(5) *Skenidioides* type.—This is a modification of the *Plectorthis* brachial apparatus, and probably is derived out of that of *Finkelburgia*. The brachiophores are very long and the supports are concave, uniting with a high median septum to form a cruralium. The sockets are defined by concave fulcral plates.³² This type is not confined to the impunctate orthids but occurs also in *Linoporella* (see pl. 10, figs. 8, 10, 12).

(6) *Schizophoria* type (see pl. 23, figs. 7, 8, 21; pl. 24, fig. 3).—Here the brachial apparatus simulates that of *Hebertella*, but differs chiefly in having vertical or widely flaring and never convergent brachiophore supports. The brachiophores are rather long and shaped like the tusk of a boar. The sockets are defined by fulcral plates (see pl. 23, figs. 18, 21). This type is seen to perfection in *Pionodema*, *Schizophoria*, and *Enteletes*, and characterizes the Schizophoriidæ.³³

In the (7) *Dalmanella* type (see pl. 17, figs. 2, 31; pl. 18, figs. 23, 29), the brachiophores are flattish divergent blades placed obliquely to the vertical. The socket is formed by the outer sloping

³¹ Cooper, Jour. Pal., vol. 4, 1930, p. 371.

³² See Kozłowski, Pal. Polonica, pt. I, 1929, p. 48, t. fig. 5, for illustration of this type.

³³ Cooper, op. cit., p. 374.

face of the brachiphore, fulcral plates being absent. The brachial apparatus is supported by adventitious shell substance only, deposited on the inside surface of the brachiphores and under the antero-dorsal edge. This gives, in old shells, a cuplike appearance. This type of brachiphore is best seen in *Levenea*, *Dalmanella*, *Cariniferella*, etc.

(8) *Parmorthis* type (see pl. 21, figs. 3, 13).—The brachiphores here are supported by short divergent plates and the socket is defined by a concave fulcral plate. This type is found in *Parmorthis*, *Mendacella*, etc.

(9) *Wattsella* type (see pl. 22, figs. 9, 22, 23, 25, 29).—Like the preceding except that the brachiphore plates are subparallel or convergent and unite with the median ridge. Fulcral plates are present.

(10) *Heterorthis* type (see pl. 20, figs. 19, 20).—In this group the brachiphores are dalmanellid-like, but supported by a deposit of adventitious substance spreading from the notothyrial platform and the floor of the valve under the dorsal edge of the brachiphore. This is clearly a modification of the *Dalmanella* type and is seen also in *Smeathenella*, *Reuschella*, and *Harknessella*. In *Rhipidomella* and its allies, support of the brachiphores is by means of adventitious substance from the floor of the valve, which unites with the dorsal edge of the brachiphore; here, too, there also is not uncommonly a rather long sharp crural process extending from the brachiphore.

CRURALIUM AND PSEUDOCRURALIUM

A cruralium is not often seen in the Orthoidea, but some stocks have developed it, as the Skenidiidæ, Mystrophoridæ, and Linoporellidæ. Some of the Plectorthidæ have a sessile cruralium. In the Billingsellidæ and Orthidæ a pseudocruralium is not uncommon; it is the same structure that we have called notothyrial platform.

SEPTA

The dorsal valve of the Orthoidea is almost never without some sort of axial thickening to strengthen the valve between the adductor muscles. This thickening is usually in the form of a low broad ridge, as in *Hesperorthis* (see pl. 4, fig. 17), and rarely takes the form of a narrow septum. In a few families and genera the median septum forms a prominent partition which divides the valve into equal halves. Such is the case in the Skenidiidæ, and also in *Mystrophora*, where the septum is so high as nearly to reach the inner surface of the ventral valve.

The median ridge of most orthids is clearly the homologue of the median septum of the Rhynchonellacea, and in the Paleozoic these shells are scarcely ever without an axial thickening. Aberrant genera such as *Porambonites* and *Lycophoria* are unique in not possessing a median septum.

MUSCULATURE

The individualization of the musculature of the dorsal valve is fraught with the same difficulties as that of the ventral valve. In well preserved specimens there are usually the distinct scars of eight muscles, but in a few species two additional scars are distinguishable. Most prominent and usually best preserved are the four (in many genera six) adductor scars produced by the bifurcation of the two ventral adductor muscles as they pass from the ventral to the dorsal side. These form a field of variable outline usually located near the center of the valve and anterior to the notothyrial platform. These two pairs are almost invariably divided longitudinally by the median ridge and are usually separated transversely by smaller, less prominent ridges at a greater or lesser angle to the median one, thereby dividing the field into quadrants. The pair immediately in front of the notothyrial platform are the posterior adductors, and the pair farther forward are the anterior adductors.

In many genera the anterior adductor impressions are clearly divisible each into two parts (notably true in *Productorthis*, see pl. 3, fig. 11), so that there are evidently six scars in the adductor field. This third "adductor" set may represent adjustor muscles whose ventral attachments are on the pedicle and are thus not recorded by a corresponding set of impressions on the ventral valve. It is possible also that the adductor muscles trifurcate in their passage from the ventral to the dorsal valve.

Derby³⁴ early directed attention to the presence of six adductor scars in the dorsal valve of

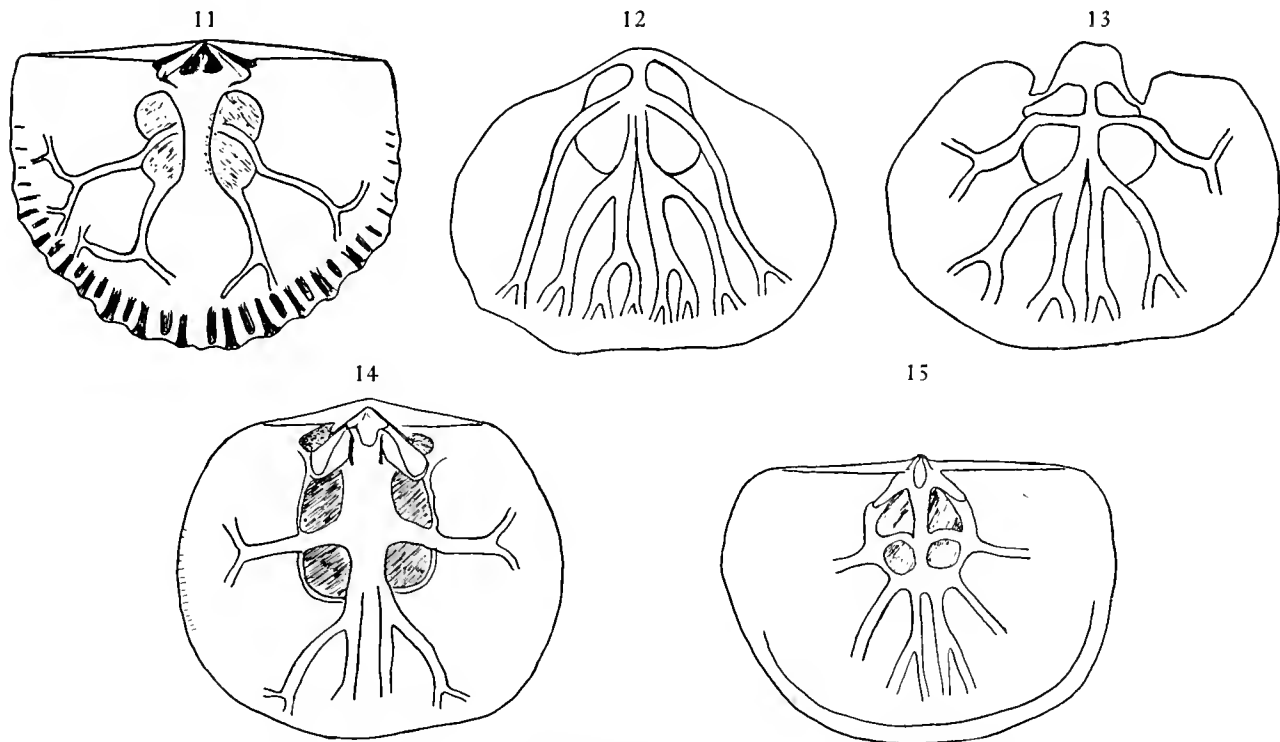
³⁴ Bull. Cornell Univ., vol. 1, pt. 2, 1874, p. 30.

Orthotichia (*Orthis* (?) *morganiana* Derby). This writer, however, was mistaken as to the true number in that genus. It is shown under *Orthotichia*, and also in our discussion of *Schizophoria*, that the posterior adductor scars migrate laterally, leaving a rather prominent space occupied by the low median ridge only. It is this space that Derby took to be the scars of a third pair of muscles.

The diductor impressions of the dorsal valve are located either on the myophore of the cardinal process or on the floor of the notothyrial cavity on either side of a linear cardinal process or septum as in *Hesperorthis* and *Dolerorthis*. In genera with a cardinal process of the *Orthis* type, it has been possible to distinguish definitely only one pair of muscles, placed on either side of the process. There is, however, a possibility that there were actually two pairs, one attached to the sides of the process and the other to the notothyrial platform next to the process. In shells with the *Dalmanella* type of cardinal process it is clear that there were two pairs of muscles attached to the myophore, as shown clearly in the quadrilobation and trilobation of the latter.

PALLIAL MARKINGS

Our study of the Orthoidea shows that a definite pattern for the pallial sinuses of the dorsal valve is fairly prevalent. In the early forms such as *Finkelburgia*, *Syntrophioides*, *Syntrophia*, *Billingsella*, and other related genera, the pallial markings in general have a radial arrangement, the trunks generally taking their origin between the adductor impressions both on the sides and in the



FIGS. 11-15.—Dorsal pallial markings. 11, *Orthis rotunda* (Pander). 12, *Schizophoria*. The usual condition in the orthoid dorsal valve is a lateral trunk extending from the space between the anterior and posterior adductors, and two trunks from the anterior end of the median ridge between the anterior adductor scars. These two trunks bifurcate immediately, giving rise to four. Cf. t. figs. 13, *Isorthis*; 14, *Levenea*; 15, *Heterorthis clytie* (Hall).

front. In later forms the radial arrangement is lost but the trunks originate at essentially the same point. In *Schizophoria* and *Isorthis* two trunks take their origin medianly between the left and right adductor sets. These extend for a short distance and then bifurcate at or near the front of the anterior adductor scars. The four resulting branches may extend directly anteriorly as in some species of *Schizophoria* (t. fig. 12), or may run obliquely as is more usual. In addition to these trunks and their subsidiary branches, a lateral trunk originates between the anterior and posterior adductors, and extends directly laterad as in *Isorthis* and *Levenea* (t. figs. 13, 14). In some species

of *Schizophoria* the low transverse ridge dividing the anterior adductors from the posterior ones is oblique, being directed antero-laterally; in such the lateral pallial trunks extend in the same direction as the adductor ridge, thus giving rise to six subparallel trunks.

Our studies show that in the present state of our knowledge not much taxonomic importance can be attached to the dorsal pallial sinuses, because of the absence of marked variation, and also because of the rarity of specimens in which they are preserved.

MICROSTRUCTURE OF THE SHELL

The orthoid shell of the Middle Ordovician, as shown by Sardeson,³⁵ consists of two calcareous layers as follows: (1) an outer, thin, first or primary, non-fibrous layer that grows at the margin of the shell only. It grows at an equal rate along the whole hinge, and elsewhere around the periphery at an increasingly greater rate toward the front. It is this first layer that determines the general outline and convexity of both valves, the folds and sulci and the plications. Sardeson erroneously calls this primary calcareous layer the "epidermis," but in living brachiopods the thin chitinous outer skin has long been known as the epidermis or periostracum and it covers the whole of the shell. Such an epidermis undoubtedly also existed in the ancient brachiopods, but all trace of it has been lost in fossilization. It is to this external chitinous skin that the term epidermis should be restricted, and Sardeson's "epidermis" is the thin lamellar layer mentioned on an earlier page.

(2) Sardeson next points out that inside the primary lamellar non-fibrous layer there is a much thicker one composed of prisms or fibres of calcite, which are directed obliquely forward and inward with respect to the whole shell. They are based against the lamellar layer and terminate upon the inner surface of the valves. The growth of this fibrous shell matter is not at the edge of the valves but upon the whole inner surface, and it is deposited by the mantle proper. This fibrous layer thickens the valves more and more, obliterates the plications and other inequalities, and often thickens the articulating and brachiophore structures. When the shell is endopunctate, it is this fibrous layer that is perforate, due to the shell's growing around the minute and threadlike papillæ on the outer surface of the mantle and adhering to the inner surface of the outer non-fibrous lamellar layer.

Young³⁶ has also shown that in the genus *Productus* there are two layers, the inner one being punctate (now known not to be true) and the outer impunctate. Kozłowski, however, points out that other strophomenids are not punctate. Young also observed a similar condition in *Eichwaldia* and *Chonetes*. In the impunctate genera it is probable that a similar condition exists, that is, there is an outer calcareous layer growing only at the margins of the shell which determines the external sculpture of the valves, and this is covered on the inner surface by the main mass of the fibrous or prismatic shell. In punctate shells the primary shell matter of teeth, dental plates, apical plates, etc., is impunctate. The deltidium is said to be impunctate in punctate shells.³⁷

In Cambrian shells Walcott reports a shell structure different from those of later periods. According to him, the billingsellids and other Cambrian shells that he sectioned appear to have a granular structure throughout. To the writers, this granular shell structure, restricted to the Cambrian, always appeared anomalous. Therefore we sectioned a specimen of *B. lindströmi* from the Paradoxides zone of Sweden, and it proved to have a fibrous structure. Indeed, the fibers are clearly visible in the specimen with a low-power hand lens (pl. 29, fig. 12). We have also rephotographed one of Walcott's sections of *B. coloradoensis* and this too proved to be fibrous (pl. 29, fig. 13). The photograph of this thin section was enlarged about 30 times, whereas Walcott used an enlargement of 50 to 100 times. We believe that this latter enlargement is too great and unduly emphasizes the fractured condition of the mineralized shell. Furthermore, we found no evidence of punctæ in any

³⁵ Amer. Geol., vol. 19, 1897, pp. 92-93.

³⁶ In Davidson, Brit. Foss. Brach., Suppl. to Carb. Brach., vol. 4, 1874, pp. 296-302.

³⁷ In regard to this statement, the writers wish to say that they have studied but one punctate shell which has a deltidium (*Kaysarella*), and unfortunately the one specimen studied was too mineralized to show whether or not the deltidium was punctate. Beecher's statement that the deltidium is impunctate in punctate shells loses force in the light of Kozłowski's recent work (1929), in which the latter shows that the supposed punctæ of the Strophomenacea are in reality granule formed by rods of crystalline substance in the shell. Since the Strophomenacea are (excluding the Clitambonitidæ) the chief deltidium-bearing shells, the anomaly emphasized by Beecher may after all not prove to be so important as he thought.

of the Cambrian shells studied, nor could we find any in Walcott's sections, although they are reported in *Billingsella*, *Huenella*, and *Syntrophia*. All of the billingsellids and other Cambrian articulates that we studied have the essential structure of *Orthis* and *Clitambonites*. There is therefore no reason to suspect that the shell structure in the oldest genera is different, and our evidence favors the view of a uniform shell nature and growth of the orthids since early Cambrian time. Furthermore, we find no punctate (endopunctate) shells in the Cambrian and Ozarkian, and this type of shell is first seen in the dalmanellids (of the Chazy), which probably had their origin in early Ordovician time (Canadian).

Since brachiopods were first studied, investigators have noticed minute perforations in the inner and outer surfaces of the test. The present observations show that these perforations are of two main sorts and that they may be grouped into two divisions, as follows:

EXOPUNCTÆ.—Pores of this type are readily visible on the unabraded exterior, i. e., in the outer lamellar layer. They do not, however, penetrate far into the interior of the shell substance and never pass completely through the fibrous test. Such pores are especially well exhibited by *Paurorthis* and have frequently been mistaken for true punctæ (endopunctæ). They are also visible in *Valcourea*, *Doleroides*, *Hebertella*, *Rhipidomella*, and many other genera. In occurrence the exopunctæ are sporadic within a genus and they are not confined to shells of the "impunctate" type. In *Valcourea*, *Doleroides*, and some other genera, the exopunctæ appear as perforations in tiny granules on the ribs.

ENDOPUNCTÆ.—These are pores that are found only in the fibrous layer of the test, extending from the inside but never appearing on the surface when the outer lamellar layer is present. On the inside they are common to the whole surface of the shell, but when the shell is costellate the pores are concentrated into rows toward the exterior.

VALUE OF PUNCTATION IN TAXONOMY

Some European authors regard the endopunctæ as important in the establishment of species among living terebratulids and other punctate shells. Since the size and arrangement of the pores is quite uniform, when the same portions of different shells are compared, a difference in pattern is believed to be of specific value. The idea has not, however, found application in this country.

Among the orthids, punctation is of great generic value, since certain types of internal structure may be correlated with the endopunctæ. The oldest known endopunctate shell occurs in the Middle Ordovician (Chazy) but from the internal structure of some Lower Ordovician (Beekmantown) genera, this type of punctate shell must occur at least that early. It appears evident at this time that the punctate forms arose out of impunctate ones, but whether the punctate stock, once arisen, remained persistent, or whether punctation was invented many times, has yet to be determined; it would appear that both views are tenable.

OLD-AGE CHARACTERS

An important feature of the inside of a brachiopod shell is the internal thickening, which is a consequence of age, since the mantle continues to secrete shell matter throughout life. This addition of extra testaceous substance may so alter the internal features, muscle fields, and cardinalia in old individuals as to suggest other genera than the one actually under observation. In the ventral valve the chief alterations are in the obsolescence of the dental plates and the development of a pseudospondylium. Hall and Clarke record the lack of dental plates as one of the generic features of *Orthorhynchula*, but in young shells of *O. linneyi* and in *O. ottawaensis* (Bills.) there are prominent dental lamellæ. The development and importance of the pseudospondylium and spondyloid are discussed under *Glossorthis*, *Linoporella*, *Porambonites*, and other genera having this feature.

In the dorsal valve, adventitious tissue is commonly utilized for the support of the brachio-phores, as is well exhibited in the Clitambonitidæ (see figures of *Estlandia*). We have laid chief stress in classification, however, upon the primary or youthful structures, and these have guided in making our family groupings. The different modes of deposition of extra shell matter are useful in some instances in showing relationships, but are more often deceptive.

PART IV. THE GENERA OF THE SUBORDER ORTHOIDEA

The superfamily Orthacea erected by Walcott and Schuchert in 1908 has grown to large proportions in the way of genera. Among these the presence of an impunctate (may be exopunctate) or a punctate (always endopunctate) shell is now seen to be of much significance in taxonomy, and the genera of the old division "Orthacea" are now known to be separable, on the basis of punctation and certain internal features of the shells, into three superfamilies, namely, (1) Orthacea as here restricted, (2) Clitambonacea (formerly included in the Pentameracea), and (3) Dalmanellacea. Out of the Orthacea came the (4) Syntrophiacea, which may have given rise to the (5) Pentameracea; both are now included in the new suborder Pentameroidea. All of these superfamilies are impunctate with the exception of the Dalmanellacea, which are internally punctate (endopunctate).

As the superfamilies Orthacea, Clitambonacea, and Dalmanellacea are closely linked genetically and have an external expression in common, i. e., transverse shells with wide hinge-lines, more or less prominent interareas, and usually open delthyrium, it is desirable to combine them into a new suborder, Orthoidea. On the other hand, the Syntrophiacea and the Pentameracea tend more and more with time to lose their orthid expression and to become elongate and rostrate shells with decidedly different cardinalia, and accordingly are combined into the new suborder Pentameroidea.

Therefore when we write "orthids," we refer to Orthacea, dalmanellids = Dalmanellacea, clitambonitids = Clitambonacea, syntrophiids = Syntrophiacea, and pentamerids = Pentameracea. "Orthoids," on the other hand, refers to the Orthoidea, and "Pentameroids" to the Pentameroidea.

The suborder Orthoidea ranges, so far as known, from the Lower Cambrian to the close of the Permian, whereas the Pentameroidea begin in the Upper Cambrian and die out with the Devonian.

Ulrich¹ in discussing the musculature of the Ordovician orthoids in comparison with those of the Cambrian, foreshadows the classification developed in this book when he says that a "natural division" of the orthoids into two families is possible as follows:

(1) Ventral muscular area small, obovate or obcordate; adductors reaching front margin of area (*Orthis* s. s. [= *Hesperorthis*], *Plectorthis*, *Platystrophia*, *Hebertella*, *Orthostrophia*, *Dalmanella* [the only genus that we do not include in the impunctate superfamily. This is the foreshadowing of our superfamily Orthacea, now seen to be most easily distinguished on the basis of an impunctate test]) . . . (2) Ventral muscular area large, bilobed or elliptical; adductors proportionately small and more or less completely inclosed anteriorly by the flabellate diductors (*Heterorthis*, *Platymys*? *deflecta* group, *Dinorthis* [the last two genera we think are out of place here and are best referred to the Orthacea], *Bilobites*, *Rhipidomella*, *Schizophoria*, *Orthotichia*). [This division includes in the main our Dalmanellacea.]

Superfamily ORTHACEA Walcott and Schuchert 1908

Primitive Orthoidea of early Cambrian time. A prolific stock with the test always impunctate (we do not agree with Walcott's observations to the contrary). Shells usually multicostellate, rarely costate and even more rarely smooth or nearly so; nearly always with more or less prominent interareas in both valves, and wide hinge-lines; deltidia and chilidia sporadic; with a simple cardinal process except in primitive genera, where there is none; spondylia rarely developed, pseudospondylia not uncommon.

Range: Earliest Cambrian into Devonian.

Includes the families:

| | |
|-----------------|-----------------|
| Nisusiidae | Porambonitidae |
| Protorthidae | Lycophoriidae |
| Billingsellidae | Finkelburgiidae |
| Eoorthidae | Plectorthidae |
| Orthidae | Skenidiidae |
| Dinorthidae | |

The evolution is thought to be as shown in Table 1.

Family NISUSIIDÆ Schuchert and Cooper 1931

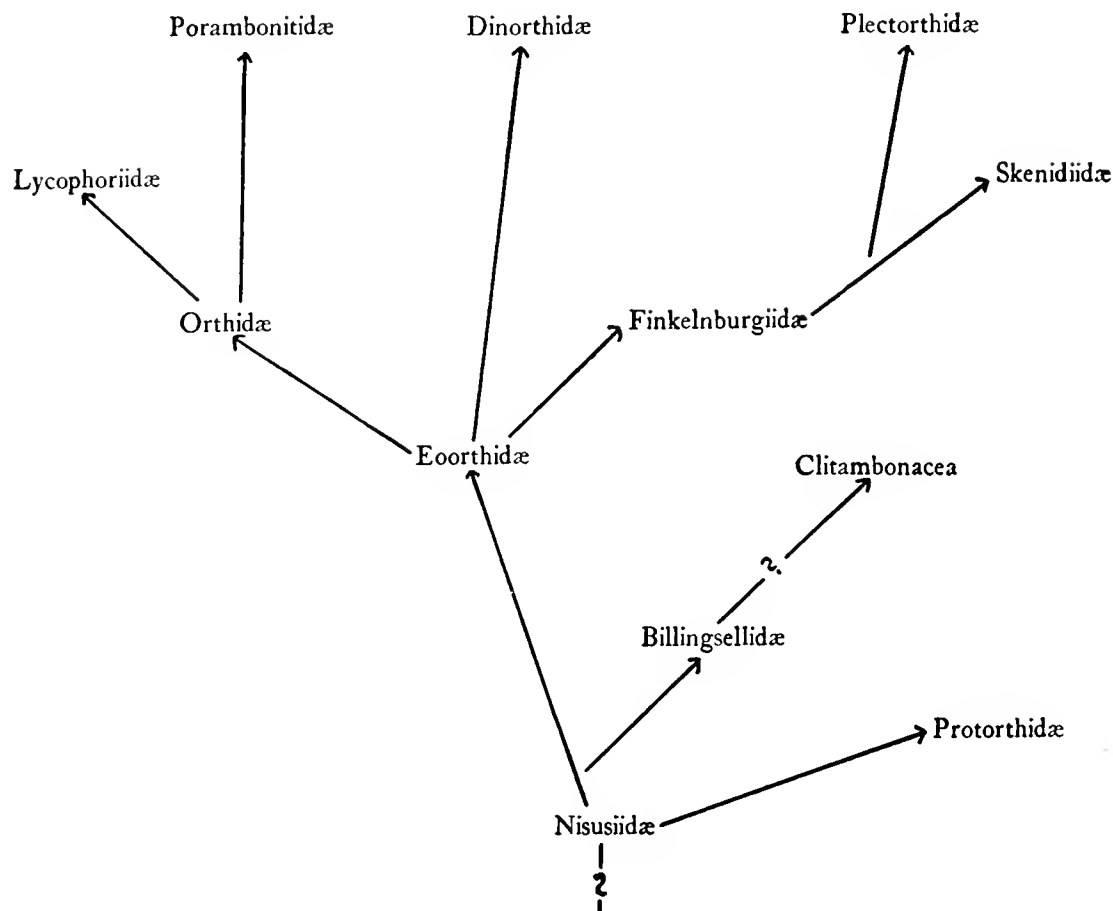
(Nisusiinae Walcott and Schuchert 1908, Walcott 1912, Schuchert 1929)

The most primitive of the known Protremata and Orthacea, having a well developed deltidium with an apical foramen in the genotype, but no dental plates. Shell probably very thin. In the dorsal valve there is a chilidium, and the brachiophores are rudimentary and similar to those of *Eoorthis* or *Billingsella*. No cardinal process is present in *Nisusia*, and a rudimentary one only in *Jamesella*.

The family embraces the genus *Nisusia*, and for the present *Jamesella* is also placed here, though its origin remains unknown.

¹ In Walcott, Camb. Brach., 1912, p. 308.

Table 1



DISCUSSION.—Walcott has always regarded *Nisusia* as the most primitive known representative of the Protemata, it being also the oldest member of this order, and to this we agree, with the statement that it appears to be the progenitor of the Orthacea. *Nisusia* appears late in the Lower Cambrian and vanishes with the Middle Cambrian. *Jamesella* is a European stock of another origin and of the later Cambrian. Possibly out of *Nisusia* came *Protorthis* of the Middle and Upper Cambrian, while the older *Loperia* is of another genetic line. As yet we do not know the origin of *Swantonina* of the Lower Cambrian, unless it be out of *Nisusia*, and this doubt is due to lack of knowledge of the dorsal interior. Since *Swantonina* has no spondylium it may not be an orthid at all, and hence it is not at all certain that this genus gave rise to the Syntrophiacea. Walcott says that *Swantonina* may have been the progenitor of both the syntrophiids and *Protorthis*,² but in this we can not concur.

² Camb. Brach., 1912, p. 320.

Genus NISUSIA Walcott 1905, emended

Pl. 1, figs. 16, 20

Walcott, Proc. U. S. Nat. Mus., vol. 28, 1905, p. 247;
Camb. Brach., 1912, p. 725, pl. 100, figs. 1-1j,
2-2c, t. fig. 6.

GENOHOLOTYPE: *Orthisina festinata* Billings 1861,
Pal. Foss., vol. 1, p. 10, figs. 11-12.

DESCRIPTION. *Exterior*.—Subquadrate to semi-oval, unequally biconvex, with the dorsal valve the more convex. Hinge-line straight, usually as great as, or greater than, the greatest width of the shell; cardinal extremities usually acute, anterior commissure faintly uniplicate; ventral sulcus shallow; ventral interarea broad, strongly apsacline to procline; deltidium well developed, strongly convex, but only partially covering the delthyrium, perforated at the apex. Dorsal interarea anacline, notothyrium more or less well developed. Chilidium present. Surface costellate, crests of costellæ provided with prominent spines

in the genotype and other species. Micro-structure of the shell not definitely known, probably fibrous, impunctate.

Ventral interior.—Delthyrial cavity obsolete; teeth very rudimentary; dental plates absent, ventral muscle-scars not visible.

Dorsal interior.—Notothyrial cavity very shallow; notothyrial callosity confined, without a cardinal process, and not produced forward as an axial ridge or thickening. Brachiophores bladelike thickenings along margins of notothyrium. Adductor scars appearing as two divergent, elongate impressions anterior to the notothyrial callosity.

GEOLOGICAL RANGE.—Late Lower and early Middle Cambrian.

AMERICAN SPECIES³

Billingsella alberta (Walcott) 1888

B. festinata (Billings) 1861

B. transversa (Walcott) 1886

Nisusia burgessensis Walcott 1924

? *Billingsella bivia* Walcott 1912

? *B. orientalis* (Whitfield) 1884

? *Nisusia* (*Jamesella*) *amii* Walcott 1905

? *N. (J.) erecta* Walcott 1905

? *N. (J.) lowi* Walcott 1908

? *N. (J.) nautes* (Walcott) 1905

? *N. (J.) spencei* (Walcott) 1905

? *N. (J.) utahensis* Walcott 1905

DISTINGUISHING CHARACTERS.—The genus *Nisusia* is characterized especially by the biconvex profile of the valves, the well developed deltidium with apical perforations (in the genotype), a chilidium, a lack of dental plates and of a cardinal process, and very primitive cardinalia. Walcott (1912) regarded it as the most primitive of known Protremata.

DISCUSSION.—Since *Nisusia* is the oldest known articulate brachiopod of the Cambrian, it has great taxonomic importance. Accordingly the species of the genus have, perhaps, the most primitive structure. The valves are biconvex, the dorsal having as a rule greater convexity. The ventral valve has a prominent sulcus and the surface of the shell is marked by costellæ which increase both by intercalation and by bifurcation. In the genotype and some of the other species the crests of the costellæ are provided with prominent spines. This spinose surface Walcott considered as the dis-

tinguishing feature between *Nisusia* and *Jamesella*, but it appears to be of doubtful generic importance, since the generic characters should be mainly the more fundamental internal ones.

The interareas are well developed on both valves and somewhat extravagantly on the ventral one. The elongate ventral interarea, combined with the prominent deltidium, might lead one to suspect that he was dealing with a member of the Clitambonitidæ, but this is not true. The deltidium is strongly arched, especially at the wide end, and does not cover the delthyrium completely. The arching is greatest at the open end of the deltidium, the margin of which is strongly concave toward the beak. The apex of the ventral shell in all specimens of *N. festinata* (Bills.) is broken, suggesting that there was an open foramen which is now filled with matrix, hence the destruction of the beak in internal molds. In any event, the actual margin of the foramen was not observed. It is well to emphasize again that the deltidium of *Nisusia* is well developed, since one might expect the delthyrium in so primitive an articulate brachiopod to be a completely open one. We therefore see that in this very early development of the deltidium and chilidium there is great value in classification, as first pointed out by Beecher.

The interior of the ventral valve shows surprisingly few characters, but this may be due to the thinness of the valves. Walcott says that these shells have "dental plates that extend outward, also inward, forming on the inside a shallow spondylium." We saw no such structures in the specimens studied, and in our opinion *Nisusia* does not possess a pseudospondylium, or any structure even remotely similar to a spondylium, nor do dental plates occur in the genotype, *N. festinata*. If such plates were present, the internal molds would show as indentations or tracks representing the position of the plates. Squeezes, however, do show slight thickenings along the delthyrial margins, which may indicate incipient dental plates or the growth tracks of the teeth. The explanation of all this is that Walcott's reference to dental plates (pl. 100, fig. 1f) and a pseudospondylium in *N. festinata* was inadvertently made on a dorsal valve. The cardinalia of *Nisusia* do, in some degree, resemble a cruralium (see his p. 728), and his "spondylia" in *Nisusia* may have been incorrectly identified in dorsal valves. Traces of musculature occur rarely in the ventral molds, but are too faint to make out their nature.

The internal morphology of the dorsal valve of *Nisusia*, like that of the ventral valve, is misunderstood. Walcott has described a cruralium, but it may be questioned whether this structure exists in any of the Cambrian genera. The brachiophores are flattened plates like those of *Billingsella* or *Eoorthis*, making the notothyrial margin, and are supported by adventitious shell deposit that extends from the floor of the notothyrial cavity. These plates are situated oblique to the dorsal

³ Generic designations used in these lists are taken from the following sources:

For American species prior to 1897, Schuchert, Bull. 87, U. S. Geol. Surv., 1897.

For Cambrian species from 1897 to 1912, Walcott, Mon. 51, U. S. Geol. Surv., 1912.

For American Ordovician and Silurian species from 1897 to 1915, Bassler, Bull. 92, U. S. Nat. Mus., 1915.

Other species are, in the main, cited under their original generic designation.

direction, and the margins of the interarea overlap them, leaving a long groove on their outer side which serves as the dental sockets. A chilidium is present in several species, but there is no cardinal process. The only evidence of the adductor tracks is two elongate, divergent depressions just anterior to the notothyrial callosity.

From the above it is evident that it has been necessary wholly to revise Walcott's list of species referred to *Nisusia*, with the result that but four are left unquestionably by us in this genus. *N. compta* (Tate) of South Australia varies widely from *Nisusia* in the shape of the valves. It is syntrophiid in form and suggests *N. oriens* Walcott 1924. Both these species should be referred to another genus.

Genus JAMESELLA Walcott 1905

Pl. 1, fig. 24

Walcott, Proc. U. S. Nat. Mus., vol. 28, 1905, p. 252; Camb. Brach., 1912, p. 731, pl. 101, figs. 1-1h.

GENOHOLOTYPE.—*Orthis perpasta* Pompeckj 1896, Jahrb. geol. Reichs. Wien, vol. 45, pp. 515-516, pl. 15, figs. 15-18.

DESCRIPTION. *Exterior*.—Transversely subquadrate; hinge-line straight, cardinal extremities usually obtuse. Lateral profile subequally biconvex. Fold and sulcus not stabilized. Ventral interarea long, curved, strongly apsacline; delthyrium open or covered by a convex deltidium. Dorsal interarea short, moderately anacline; notothyrium open. Surface usually multicostellate. Microstructure of shell unknown.

Ventral interior.—Delthyrial cavity deep, dental plates rudimentary (?); muscle area wide; adductor track subtriangular, longer than the diductor scars; diductor impressions wide, attached on the sides of the delthyrial cavity; pallial depressions on the outside margins of the diductors, but their anterior continuations are not visible.

Dorsal interior.—Notothyrial cavity moderately deep, brachioophores billingselloid, dental sockets small; cardinal process linear or rudimentary; adductor scars unknown.

GEOLOGIC RANGE.—Walcott (1912) says that *Jamesella* occurs in the Lower Cambrian, but the actual deposits having the conglomerate pebbles with fossils are of Middle Cambrian time. The genus is very poorly known and none of the American species referred to it conforms to the structure of the genotype. As here redefined, *Jamesella* is restricted to the Middle Cambrian of Bohemia, most of the American Lower Cambrian species placed here by Walcott being better referred doubtfully to *Nisusia*.

EUROPEAN SPECIES

Nisusia (Jamesella) kuthani (Pompeckj) 1896

N. (J.) perpasta (Pompeckj) 1896

N. (J.) perpasta macra (Pompeckj) 1896

N. (J.) perpasta subquadrata (Pompeckj) 1896

DISTINGUISHING CHARACTERS.—Walcott distinguished *Jamesella* from *Nisusia* chiefly by the absence of external spines in the former. More fundamental, however, are the presence of pronounced muscle-scars showing a rather wide adductor track, and the rudiments of pallial marks similar to those usually seen in *Billingsella*. In the dorsal valve the cardinalia are billingselloid, so far as can be determined from squeezes of the genotype specimens. The interior characters are those rather of Middle Cambrian than of Lower Cambrian time.

Family PROTORTHIDÆ Schuchert and Cooper 1931

Primitive specialized Orthacea with a very short free concave plate, evidently a free spondylium; there are no dental plates nor is there a deltidium or chilidium; the cardinalia are like those of *Billingsella*, and a cardinal process is absent.

The family embraces *Protorthis* Hall and Clarke and *Loperia* Walcott, both of the Middle Cambrian of New Brunswick and Nova Scotia.

DISCUSSION.—Walcott (1912, p. 317) thinks that *Protorthis* arose in the Lower Cambrian out of the stock that gave rise to *Nisusia*, and to this we agree.

Genus PROTORTHIS Hall and Clarke 1892

Pl. 1, figs. 12, 14

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, p. 231, pl. 7a, figs. 14-21.

Walcott, Camb. Brach., 1912, p. 738, pl. 99, figs. 1-1g.

GENOHOLOTYPE.—*Orthis billingsi* Hartt 1868, in Dawson, Acad. Geology, 2d ed., p. 644, fig. 223.

DESCRIPTION. *Exterior*.—Shell usually small, thin-shelled, transversely subquadrate or semicircular, hinge-line straight, usually equal to the greatest width of the valves; cardinal extremities angular; lateral profile subequally biconvex. Ventral interarea long; delthyrium open. Dorsal interarea short; notothyrium open. Surface multicostellate. Microstructure fibrous?, impunctate.

Ventral interior.—Teeth small, delthyrial cavity defined by a free spondylium, probably for pedicle muscle attachment. Muscle-scars not visible on spoon or floor of valve.

Dorsal interior.—Notothyrial platform very shallow, confined and without a cardinal process; chilidium absent; brachioophores like those of *Billingsella*, short; median ridge absent.

GEOLOGIC RANGE.—Middle Cambrian of New Brunswick.

SPECIES

Billingsella billingsi (Hartt) 1868

B. latourensis (Matthew) 1886

B. quacoensis (Matthew) 1886

? *Eoorthis hastingsensis* Walcott 1905

P. (?) *hunnibergensis* and *P. wingi* of Walcott can not be placed in any Cambrian genus. *P. helena* and *P. laevis* of the same author may be syntrophiid.

More recently, Walcott⁴ has also referred two Ordovician shells, *P. ioues* and *P. porcias*, to this genus. Neither has a free spondylium or any structure approaching it. Furthermore, both species are composite, including representatives of *Archæorthis* and probably of *Taffia*.

DISTINGUISHING CHARACTERS.—*Protorthis* externally resembles *Eoorthis* with its rather large costellæ, but the unsupported short spondylium of the ventral valve is an important feature in its identification.

DISCUSSION.—The preservation of the New Brunswick Middle Cambrian *Protorthis* is not good. The specimens occur in a soft and much distorted shale and accordingly are much crushed. It is, however, possible to distinguish, in molds of the interior, rather small teeth for articulation of the valves, and thickenings along the delthyrial margins which are the tracks of the forward growth of the teeth.

The most interesting and important internal feature in *Protorthis* is the very short and small spondylium that hangs free in the delthyrium. Hall and Clarke⁵ say correctly that the cardinal area "is transected by a broad delthyrium which is closed below by a concave plate apparently produced by the union of the dental lamellæ, which are not continued to the bottom of the valve." In *Protorthis* the spondylium is variable in length; in some species it is a narrow shelf under the posterior lateral margins of the delthyrium, and in others it is a spoon-shaped plate two-thirds the length of the delthyrium. Since the function of the true spondylium is to furnish attachment for the diductor and adductor muscles, one should expect to find scars on the spoonlike plate. No such scars have been seen on the spondylium, nor have definite scars been discovered on the floor of the valve beneath the spondylium. Evidence is therefore lacking as to the function of this peculiar structure. Such a plate as this is unknown elsewhere among the orthoids. Among the pentamerids a free spondylium is known and its origin can be traced to the resorption of the median supporting septum. Such an origin can not be maintained for the spondylium of *Protorthis* because there is no known spondylium-bearing (with a median septum) ancestor

from which it could have been developed. Furthermore, the orthoid brachiopods older than *Protorthis* were not provided with dental lamellæ. It is here suggested that in *Protorthis* we have one of the earliest developments of dental plates, but in this instance the dental lamellæ grew toward each other and united instead of growing directly ventrally to the floor of the valve.

The morphology of the dorsal valve of *Protorthis* is not unlike that of *Nisusia* and *Billingsella*, since the former has very primitive cardinalia and a cardinal process is wanting. No definite evidence of the musculature is known.

It has been customary, since the publication of *Protorthis* by Hall and Clarke, to say that it has a punctate shell. The evidence for this statement is found in the presence of fine papillæ on the molds of the exterior or interior. Although papillæ are suggestive of punctæ, a thin section of the shell in the Schuchert Collection fails to reveal true punctæ (endopunctæ). On the other hand, as no Cambrian articulate brachiopod is definitely known to have a punctate shell (endopunctate), it is hardly to be expected that *Protorthis* has such.

Protorthis is unlike any other known genus and therefore appears to be an early specializing stock which gave rise to no other groups.

Genus *LOPERIA* Walcott 1905

Walcott, Proc. U. S. Nat. Mus., vol. 28, 1905, p. 287;
Camb. Brach., 1912, p. 744, pl. 99, figs. 5-5j.

GENOHOLOTYPE.—*Protorthis* (*Loperia*) *dougaldensis* Walcott 1905.

DESCRIPTION. *Exterior.*—Outline subquadrate, hinge-line straight, cardinal extremities obtusely subangular; lateral profile resupinate. Ventral interarea long, strongly apsacline; delthyrium open. Dorsal interarea short, procline or faintly anacline; notothyrium narrow, open. Surface multicostellate. Microstructure probably fibrous impunctate.

Ventral interior.—Precisely as in *Protorthis*.

Dorsal interior.—Crural bases very short, notothyrial platform small, bearing a very low, thick cardinal process. Median elevation low.

GEOLOGIC RANGE.—Middle Cambrian. Only known species, *L. dougaldensis* Walcott of Cape Breton, Canada.

DISTINGUISHING CHARACTERS.—*Loperia* is characterized by the same internal features as *Protorthis*, but differs in having a strophomenoid lateral profile or convexo-concave shell. The ventral valve has strong teeth and a free spondylium, but no clear evidence of musculature was seen on it. In the dorsal valve, the

⁴ Smiths. Misc. Coll., vol. 67, no. 9, 1924, pp. 503, 504.

⁵ Pal. N. Y., vol. 8, pt. 1, 1892, p. 231.

cardinalia are more strongly developed and there is a low thick cardinal process; nothing of muscle marks was seen.

DISCUSSION.—Walcott states that the shell of this genus is punctate, and the evidence is based on the presence of papillæ on the internal and external molds. If these indicate endopunctæ, they should be confined to the internal molds; besides, they are coarser than is common for punctæ in punctate shells. We can not explain these supposed pores either as fortuitous or as anatomical features. We incline toward the former view.

Family BILLINGSSELLIDÆ Schuchert 1893

Primitive costellate Orthacea, usually with a deltidium and chilidium; there is no spondylium, since the dental plates remain discrete, but there may be a pseudospondylium. The ventral muscles are clearly differentiated into broad adductor and well marked diductor tracks. Ventral pallial sinuses widely divergent. In the dorsal valve the brachiophores are short, flat, oblique plates, placed under the palintrope. Cardinal process present or absent; when present, a simple vertical plate. As now constituted, the family has but the one genus, *Billingsella*.

DISCUSSION.—Hall and Clarke⁶ say that *Billingsella* "may have served as a point of departure for the Orthidæ and Strophomenidæ." Walcott⁷ is correct in saying that the general resemblance of the Cambrian eorthids to certain Ordovician Protremata is striking and the lines of descent suggestive. This is seen not only in the family Billingsellidæ, but as well in its descendants the Finkelnburgiïdæ, Plectorthidæ, Orthidæ, and the Clitambonacea and Syntrophiacea. The Strophomenacea are structurally foreshadowed here, but these apparently did not originate directly out of the Billingsellidæ but out of one of the later families, probably the Orthidæ, during the Lower Ordovician, since the earliest known forms occur in the Middle Ordovician (Chazy). In this work we have not taken up a revision of the Strophomenacea for want of time, and must leave it to others.

Billingsella, as here defined, could, theoretically, have given rise to the Clitambonacea, a group now known to be closely related to *Orthis*. This superfamily is provided with pallial markings exactly like those of *Orthis* (see pl. 8, fig. 10). Furthermore, the Clitambonitidæ and Deltatreidæ retain the primitive deltidium and chilidium so well developed in *Billingsella*.

Genus BILLINGSSELLA Hall and Clarke 1892

Pl. 1, figs. 6, 10, 13, 19, 21, 25, 27; pl. 29, figs. 12, 13

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, p. 230, pl. 7, figs. 16-19, pl. 7a, figs. 7-9.

Walcott, Camb. Brach., 1912, p. 749, pl. 85, fig. 1, t. figs. 6, 66.

GENOHOLOTYPE.—*Orthis pepina* Hall 1863, N. Y. State Cab., 16th Rept., p. 134, pl. 6, figs. 23-27.

DESCRIPTION. *Exterior*.—Subquadrate or semicircular in outline, ventral valve subquadrate, dorsal valve usually transverse; hinge-line straight; cardinal extremities usually rectangular or obtusely angular, occasionally acute; lateral profile unequally biconvex; anterior commissure faintly sulcate; ventral palintrope very long, orthocline or moderately apsacline; delthyrium wide, more or less covered by a convex deltidium which in some species is perforated at the apex by a small aperture. Dorsal palintrope shorter than the ventral, strongly anacline, notothyrium wide, partially covered by a convex chilidium. Surface multicostellate. Microstructure fibrous, impunctate.

Ventral interior.—Teeth prominent and large, with strong sockets on their outer margins; dental plates strong, oblique to the vertical and widely divergent; musculature prominent and scarcely ever making a distinct pseudospondylium; diductor tracks widely divergent; adductor track forming a central triangular scar that is often more or less prominently elevated in front. Pallial marks prominent, consisting of two pairs of divergent, narrow sinuses, originating at the anterior margin of the diductors and extending forward about three-fourths the length of the valve, where they fork. In the center of the valve they define an elongate pentagonal area and laterally they bound a subreniform space. At the anterior margin innumerable secondary sinuses extend radially toward the margin.

Dorsal interior.—Brachiophores widely divergent, short, and with imperfectly defined sockets appearing as shallow cups outside the crural bases. Brachiophore bases usually somewhat obscured by adventitious shell grown about them, forming a prominent thickening in the notothyrial cavity and extending forward a short distance as a median axial thickening. Cardinal process a simple ridge between the diductor scars; adductors elongate; elliptical scars diverging from the prominent pits anterior to the notothyrial platform; a radial pallial mark extending with slight convexity from the anterior end of each adductor impression.

GEOLOGIC RANGE.—Mainly Middle Cambrian to uppermost Cambrian. There is also an undescribed species in the lower Ozarkian of North America.

AMERICAN SPECIES

Billingsella ? *appalachia* Walcott 1905

B. coloradoensis (Shumard) 1860

B. holtedahli Walcott 1924

⁶ Pal. N. Y., vol. 8, pt. 2, p. 355.

⁷ Camb. Brach., p. 300.

B. major Walcott 1905
B. plicatella Walcott 1905
B. striata Walcott 1905
Orthis pepina Hall 1863
Clitambonites planus retroflexus Matthew 1896 (looks much like *B. lindströmi*)

EUROPEAN SPECIES

Billingsella lindströmi (Linnarsson) 1876

DISTINGUISHING CHARACTERS.—The important distinguishing features of *Billingsella* are the subquadrate outline and biconvex lateral profile; ortho- or slightly apsacline, elongate and plane interareas; large teeth with low supporting lamellæ; prominent muscle marks with elongate adductor track; strong pallial trunks; primitive cardinalia; and the presence of a deltidium and chilidium.

COMPOSITION OF GENUS.—Before we proceed with the generic discussion, it should be said that Walcott in 1912 referred 20 species and 1 variety to *Billingsella*—a rather heterogeneous lot—and of these 14 are found in North America, the remainder in Norway and Sweden (3), Wales (1), Bohemia (1), and China (2). Of these 21 forms we leave but 8 (? 7) in *Billingsella* (7 in America and 1 in Sweden). Of the other 13, 2 are referred doubtfully to *Nisusia* (*bivia* and *orientalis*), 3 to *Oligomys* (*exporrecta* and *rugosicostata* of Sweden and *hicksi* of Wales), 1 to *Wimanella* (*highlandensis*), 1 to *Bohemiella* (*romingeri*) and 1 (*B. dice* Walcott) to *Deltatrete*; this leaves 5 unplaced for want of knowledge of their interior characters. It is at once apparent, therefore, that our characterization of *Billingsella* is narrower and more precise than that of Walcott.

DISCUSSION.—It is important, therefore, to define precisely the morphology of *Billingsella*, since the members of this genus and especially the genotype, together with *B. coloradoensis* (Shum.), have been widely figured and variously interpreted. Externally *Billingsella* is distinctly subquadrate in outline, but more peculiar is the very long interarea, wide delthyrium, and, in the genotype and *B. coloradoensis* at least, the prominent apically perforated deltidium. The deltidium is a discrete convex plate, but usually less convex than Walcott figures it on his plate 85, figure 1n, a figure which unfortunately has been republished very widely; it is a normal delthyrial covering that is apically perforate, and in situation and size this aperture recalls that seen in the deltidium of *Rafinesquina* or *Strophomena* more than that of the Clitambonitidæ. Further, the deltidium of *Billingsella* is clearly an arch built with its piers fastened to the inside of the walls of the delthyrial cavity just below the delthyrial margins of the interarea.

In the ventral valve the internal structures are distinctly orthoid or clitambonitoid. The dental plates are widely divergent, obliquely cemented to the floor of

the valve, and at their anterior ends are continuous with the teeth. The pseudospondylium, when developed, is a callus under the muscle attachments, and none of the species here referred to *Billingsella* has excessive thickenings at the posterior end. Walcott mentions such structures only in *B. dice* (pp. 749, 754), *B. orientalis* (p. 307), *B. exporrecta* (p. 307), and *B. highlandensis* (p. 307), but all of these species are referred by us to different genera. In Kozłowski's opinion,⁸ *Billingsella* has rudimentary spondylia, but the type of dental plates and muscle area corresponds to his spondylium discretum, which, however, is in reality not a spondylium.

The ventral musculature of *Billingsella* is essentially orthoid in plan and its most important characteristic is the elongate adductor track which expands as it grows forward and is usually slightly elevated on a low callus at its anterior end. The diductor tracks are shorter and continuous with the pallial trunks. Positive evidence of adjustor marks is lacking, as in *Orthis s. s.*, *Hesperorthis*, *Nicolella*, etc. These muscles may have been confined to the dental plates, where they are not visible, or may have been united with the diductors.

The ventral musculature of several species presents some variations from the normal type. In *B. resseri* and *B. trempealeauensis* (both of Ira Edwards MS.), the diductor tracks unite for nearly the whole length of the delthyrial cavity, restricting the adductor track to a small subpentagonal scar at the antero-median sides of the diductor marks. A similar arrangement is suggested in *B. highlandensis* (a *Wimanella*) and *Wimanella simplex* (see Walcott, pl. 87, fig. 4b, and pl. 89, fig. 2d).

One of the striking characters of *Billingsella*, and one which has been exploited considerably, is the prominent ventral pallial marks usually called "vascular" markings. These consist of two more or less strongly impressed, subparallel, narrow depressions, originating at the front ends of the diductor scars and extending antero-laterally. Near the front of the shell the subparallel trunks fork, the outer branch curving backward and extending nearly parallel to the periphery of the shell and terminating near the cardinal extremity. The inner sinuses run obliquely toward the middle of the shell, where they either die out or unite at the mid-line, forming an elongate pentagon. Near the front margin many subsidiary branches radiate from the main channel. Pallial marks similar to those of *Billingsella* are also common to other Cambrian shells, and this fundamental type can be seen, with variations, in all higher genera.

The cardinalia are very distinctive and exceedingly important from a taxonomic point of view. The brachio-phores are flattened plates set obliquely beneath the interareal margins of the notothyrium. They are

⁸ Pal. Polonica, vol. 1, 1929, p. 128.

supported by a prominent callosity or swelling in the notothyrial cavity (the pseudocruralium of Walcott), which is extended forward no farther than the middle of the valve as a low axial thickening. Articulation is accomplished by the sloping inner surface of the ventral tooth which rests on the slanting outer surface of the brachiophore. The cardinal process is a simple linear ridge, a septum between the diductor muscles, and serving also partly for muscle attachment; but the chief seat of attachment appears to have been on the notothyrial callosity.

The dorsal musculature of *Billingsella* is rather obscure, but there appear to be four adductor impressions, the posterior pair being located in the pits immediately anterior to the notothyrial platform and being somewhat larger than the anterior pair.

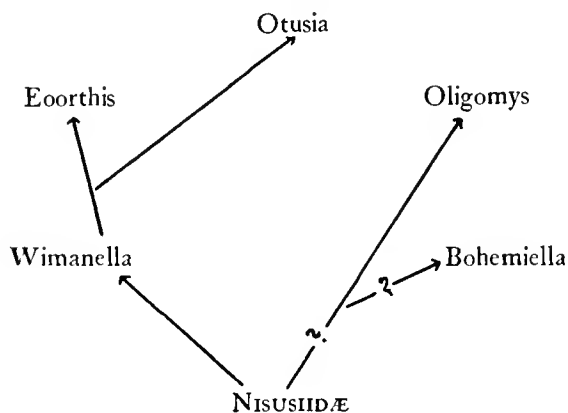
Family EOORTHIDÆ Schuchert and Cooper 1931

Orthacea wholly without deltidia and chilidia, so far as known, and with or without a cardinal process. Though not yet well understood, the family is now considered to embrace the following genera:

Wimanella Walcott
Eoorthis Walcott
Otusia Walcott
Bohemiella Schuchert and Cooper
Oligomys Schuchert and Cooper

The genetic lines are thought to be about as shown in Table 2.

Table 2



Unfortunately most of the species of the Eoorthidæ are not well understood internally, due to their poor preservation or to lack of material. Nearly all of the specimens come from limestone and accordingly most of them are exfoliated, and but rarely are the interiors of the valves nicely weathered out, as is so commonly

the case with many of the brachiopods of the Ordovician and later periods. Finally, we know the American shells best, and the European and Chinese species are regrettably few in number. On the other hand, the brachiopods of the American Lower Ordovician (Canadian) are almost unknown, and here are to be expected the connecting links between the genera of the Cambrian and the later Ordovician. Under these circumstances a final classification of the Eoorthidæ along well determined genetic lines is yet to come, and when it does, the phyletic lines into the Orthidæ and Clitambonitidæ will be better established.

Genus WIMANELLA Walcott 1908

Walcott, Smiths. Misc. Coll., vol. 53, 1908, p. 98, pl. 10, fig. 2; Camb. Brach., 1912, p. 745, pl. 89, figs. 2-2e, t. fig. 64; Smiths. Misc. Coll., vol. 67, 1924, pl. 111, figs. 2-4.

GENOHOLOTYPE.—*Wimanella simplex* Walcott 1908, an almost characterless species. Our presentation is based on the genotype and *Billingsella* (= *Wimanella*) *highlandensis* (Walc.).

DESCRIPTION. *Exterior.*—Thin-shelled. Outline subquadrate to subsemicircular; hinge-line straight; cardinal extremities obtusely or acutely angular; lateral profile subequally biconvex; ventral interarea longer than dorsal; delthyrium open; notothyrium narrow, open. Surface covered by fine concentric growth-lines and obscure costellæ.

Ventral interior.—Delthyrial cavity shallow, diductor scars large, tapering anteriorly, separated dorsally by a low ridge, which forks anteriorly about the adductor impression; pallial trunks prominent.

Dorsal interior.—Crural plates short; axial ridge low, extending forward to about the middle of the valve. Cardinal process apparently absent.

GEOLOGIC RANGE.—Lower and Middle Cambrian of North America.

SPECIES

Orthis ? *highlandensis* Walcott 1886
Wimanella ? *anomala* Walcott 1905
W. borealis Walcott 1924
W. shelbyensis Walcott 1908
W. simplex Walcott 1908

DISTINGUISHING CHARACTERS.—The name *Wimanella* may serve for Lower and Middle Cambrian nearly smooth or very finely ribbed billingsellids of the type of *W. simplex* Walcott. As stated by Walcott (1912), the genus was to embrace the older and smooth shells of the Billingsellidæ, but a study of all of his species of *Wimanella* at the U. S. National Museum shows the presence of faint radiating lines in shells conspecific with the genotype and in the actual types. Obviously, then, the characterization of this

genus as strictly smooth Billingsellidæ has little generic value. However, the name will be useful for the oldest Eoorthidæ, having finely costellate shells with interiors that approach the features of *Billingsella*.

DISCUSSION.—In choosing *Wimanella simplex* as the genotype, Walcott unfortunately selected an almost characterless shell. The material from Montana occurs in a soft shale, and since the forms are rather thin-shelled they are badly crushed and show little of the morphology. This is particularly true of the type specimen (see pl. 89, fig. 2 of Walcott 1912). The most important clue to the ventral morphology of these shells is furnished by a specimen referred to *W. simplex* (Ibid., pl. 89, fig. 2d), in which the ventral musculature consists of two large diductor tracks, closely adjacent at the posterior of the shell but divergent at the front. In the space between the antero-median margin of the diductor tracks is a low suboval elevation corresponding probably to the adductor impressions. This is exactly the same musculature as shown by the type of *Billingsella highlandensis* (see Ibid., pl. 87, fig. 4b). Here the adductor impression is not shown between the diductors but is actually present in the specimen from which the figure was drawn. This species also has prominent ventral pallial trunks as in *Billingsella*, is likewise very finely ribbed, and seems to correspond well with the concept of *Wimanella* described in this paper.

Wimanella borealis Walcott is another finely costellate species and this one too is said to have faint pallial marks, although they do not show on Walcott's figures (1924, pl. 111, fig. 2). The writers have excluded *Wimanella harlanensis* (Walc.) from this genus, since its structure, especially in the musculature of the two valves, relates it to *Syntrophia* and *Clarkella*. The placing of *Wimanella inyoensis* Walcott among the articulate brachiopods is questionable.

Genus EOORTHIS Walcott 1908

Pl. 1, figs. 23, 26, 28

Walcott, Smiths. Misc. Coll., vol. 53, 1908, p. 102; Camb. Brach., 1912, p. 772, pl. 91, figs. 1-1s, pl. 92, figs. 2-2d, 3-3e, t. fig. 7.

GENOHOLOTYPE.—*Orthis remnicha* Winchell 1886, Geol. Surv. Minn., 14th Ann. Rept., pp. 317-318, pl. 2, fig. 7.

DESCRIPTION. *Exterior.*—Shell subquadrate to transversely subelliptical; hinge-line straight, cardinal extremities usually obtusely angular; lateral profile subequally biconvex; anterior commissure sulcate; dorsal sulcus marked most clearly on the middle and dorsal part of the valve; ventral interarea broad, slightly curved, apsacline; delthyrium wide and not covered by a deltidium. Dorsal interarea short, anacline; notothyrium wide, not closed by a chilidium. Surface multi- to fascicostellate. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity shallow; teeth strong; dental plates strong, receding, continued around the lateral margins of the muscle field as a low ridge. Musculature orthoid, diductor scars triangular, adductor track median, expanding in front.

Dorsal interior.—Notothyrial cavity shallow; brachiophores consisting of flattened oblique plates attached to the roof of the valve on the surface of which the interarea rests, the whole forming the walls of the notothyrial cavity. The sockets are narrow and shallow (see pl. 1, figs. 23, 28). Notothyrial platform of adventitious shell crowded under the brachiophores to support them; cardinal process a simple ridge expanded toward the front. Median ridge wide and strong.

GEOLOGICAL RANGE.—Upper Cambrian to Ozarkian of North America.

SPECIES

Eoorthis indianola (Walcott) 1905
E. sulcata (Walcott) 1905
E. texana Walcott 1905
E. wichitaensis (Walcott) 1905
E. winfieldensis (Walcott) 1905
Orthis remnicha Winchell 1886

? *Eoorthis diablo* (Walcott) 1905
 ? *E. fascigera* Walcott 1924
 ? *E. nympha* Walcott 1905
 ? *E. ochus* Walcott 1924
 ? *Orthis desmopleura* Meek 1872

DISTINGUISHING CHARACTERS.—The generic characters of *Eoorthis* are: multicostate to multicostellate exterior, open delthyrium, receding dental plates; open notothyrium; billingselloid crural apparatus and rudimentary cardinal process.

COMPOSITION OF THE GENUS.—Before the genus *Eoorthis* was erected by Walcott in 1908 he referred the species to *Plectrothis*, a stock common in the Middle Ordovician. In 1912, when he published his monumental work on Cambrian brachiopods, Walcott made a virtual dump box of *Eoorthis*, referring to it no fewer than 33 species believed to have more or less of the external expression of the genotype, *Orthis remnicha*, but in most of them the interior is unfortunately unknown. Of these 33 species, 19 occur in North America, and after a restudy of all the species we are unable to place even generically no fewer than 18. Nine species (3 doubtful) we leave with *Eoorthis*, and refer 1 each doubtfully to *Protorthis* and *Finkelnburgia*, 2 to *Orusia* and 5 to *Archæorthis*. This then leaves unplaced 6 species in America, 6 in China, 1 in Europe, and 1 each in Australia and Argentina.

DISCUSSION.—The ventral interior of *Eoorthis remnicha* is distinctive, as it has structural parts that ally it with *Hesperorthis* or *Orthis*, and with the ancestral stock, *Billingsella*. The teeth are strong and

are placed slightly outside the delthyrial margins. In connection with the teeth there are receding dental lamellæ like those in *Hesperorthis tricenaria*. The front ends of the dental plates are continued as a callus around the margin of the muscle marks. The muscle field is placed on a slight thickening as is seen commonly in *H. tricenaria*, but there is in the type species no pseudospondylium such as occurs in *Finkelnburgia*. The muscle area is similar to that in *Billingsella* in plan but the adductor track is not so long as in that genus. On the other hand, the shell of *E. remnicha* is too thin and too strongly ribbed to preserve the main pallial sinuses.

In none of the species studied and belonging to *Eoorthis* was there seen a trace of a deltidium, and it is therefore reasonable to suppose that none of the species had one.

The dorsal valve of the genotype is much like that of *Billingsella*. The crural plates are flat, oblique, and divergent. They are supported by adventitious deposit which cements them to the valve and forms the noto-thyrial platform, and the latter supports the crural plates on their inner surfaces; the palintrope overlaps them on the ventral surfaces. The sockets are deep but very narrow, and the cardinal process is very low and linear. The median ridge is low, widening toward the front, and represents an elevation corresponding to the dorsal sulcus.

In the external forms of the valve and the internal structures one sees readily a rather strong resemblance between *Eoorthis* and the later Orthidæ. The dental plates, muscle marks, and certain details of the cardinalia of *Eoorthis* appear to bridge the structural gap between the Cambrian brachiopods on the one hand and the later orthids on the other. It is too early to state definitely the possible course of these evolutionary lines; many of the genera of the Ozarkian and Lower Ordovician (Canadian) are yet to be described.

Genus OTUSIA Walcott 1905

Walcott, Proc. U. S. Nat. Mus., vol. 28, 1905, p. 246; Camb. Brach., 1912, p. 769, pl. 93, figs. 4-4d.

GENOHOLOTYPE.—*Orthis sandbergi* Winchell 1886, Geol. Nat. Hist. Surv. Minn., 14th Ann. Rept., p. 318, pl. 2, figs. 8, 9.

DESCRIPTION. *Exterior.*—Shell small, transverse, hinge-line straight, cardinal extremities acute, commonly mucronate; lateral profile biconvex; dorsal valve provided with a prominent shallow sulcus, ventral valve with a low fold. Ventral interarea moderately apsacline; delthyrium wide, open. Dorsal interarea anacline, notothyrium open. Surface multicostellate. Test impunctate.

Ventral interior.—Teeth strong, dental plates oblique as in *Billingsella*. Muscle-scars not strongly impressed.

Dorsal interior.—Notothyrial cavity shallow, brachio-phores rudimentary as in *Billingsella*; cardinal process simple, a broad median ridge.

GEOLOGIC RANGE.—Upper Cambrian and possibly also Middle Cambrian of North America. The only species are *O. sandbergi* (N. H. Winchell) and *O. (?) utahensis* Walcott 1912.

DISTINGUISHING CHARACTERS.—The diagnostic generic characters of *Otusia*, according to Walcott, are its surface features, the nature of the delthyrium in the two valves, and the strong cardinal process and median ridge in the dorsal shell.

DISCUSSION.—*Otusia* in general is a smaller and differently shaped shell from *Billingsella*, being very transverse and alate along the hinge-line. The surface markings are more evenly spaced and rather more uniform than is usual in *Billingsella*. A deltidium and chilidium are lacking as far as present knowledge of the genus goes. In the dorsal valve the brachio-phores, notothyrial platform, and cardinal process are precisely as in *Billingsella*, perhaps a little more pronounced, but this may be due to the progressive evolution and younger age of *Otusia*.

Even though *Otusia* is very close to *Billingsella* in all its internal structures, the generic distinction appears to be valid on the basis of its external form, sculpture, and absence of deltidia or chilidia.

Genus BOHEMIELLA Schuchert and Cooper 1931

Pl. 1, figs. 1, 3, 5, 11, 18, 22

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 242.

GENOHOLOTYPE.—*Orthis romingeri* Barrande 1848, Naturw. Abh. von Haidinger, vol. 2, pt. 1, no. 5, p. 203, pl. 18, figs. 5a-d, as illustrated by Walcott (1912, pl. 90, fig. 2).

DESCRIPTION. *Exterior.*—Transversely suboval, hinge-line straight, equal to the width of the valves, cardinal extremities obtusely angular; lateral profile plano- to concavo-convex; anterior commissure slightly sulcate; dorsal sulcus broad and shallow. Ventral interarea longer than dorsal, curved strongly, apsacline; delthyrium open; dorsal interarea strongly anacline, notothyrium open. Surface multicostellate; test probably fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep, teeth small, dental plates rudimentary; muscular area faintly impressed; diductor scars on the sides of the delthyrial cavity; adductor track wide and long; pallial marks consisting of two sinuses extending directly anteriorly to near the front margin where they bifurcate, the outer branch continuing dorsally parallel to the anterior and lateral margins; the inner branches converge toward each other parallel to the anterior margin and unite toward the middle of the shell.

Dorsal interior.—Notothyrial cavity shallow; brachiophores decidedly orthoid, sharply defined, rather elongate, triangular in section, obliquely placed, forming the margin of the notothyrium, postero-ventral edge carinate; cardinal process a low carina widened slightly at its front. Diductor impressions on each side of the cardinal process; adductor impressions small pits, the posterior pair a little outside the anterior pair, which are close to the median ridge. Median ridge thick and wide, extending for half the length of the valve or more.

GEOLOGIC RANGE.—Middle Cambrian of Bohemia. The only known species, the genotype, was referred by Walcott (1912) to *Billingsella*.

DISTINGUISHING CHARACTERS.—*Orthis romingeri* differs so markedly from the genotype of *Billingsella* and all other species of that genus as to make it necessary to set it apart as the type of a new genus. Externally, the species is transverse, not subquadrate like *Billingsella*, the ventral interarea is strongly arched, and the dorsal valve nearly flat or concave. The interior of the ventral valve is not strikingly different from that of *Billingsella lindströmi* except in detail; in *Bohemiella* the inside pallial trunks unite in a broad curve, whereas in *Billingsella* they unite in a sharp V. In the dorsal valve, however, there are striking and important differences. The notothyrial cavity is very shallow; the brachiophores are long and thin, projecting into the valve as in *Hesperorthis*. In the genotype of *Billingsella*, the brachiophores are rudimentary and not so well developed as in *Bohemiella*. The median ridge in the latter is broad and thick and extends a short distance in front of the middle. The posterior adductors are situated a little outside the anterior pair and are slightly smaller.

DISCUSSION.—There is an interesting dorsal valve in the U. S. National Museum collection (see Walcott 1912, pl. 90, fig. 2k), showing old-age characters in the thickening of the shell, and in the development of bulbs of adventitious substance on the distal extremities of the brachiophores. In this specimen the posterior part of the valve has become so thick that the adductor muscles have migrated forward and occupy the front half of the valve. On the inside of the free end of the brachiophores the bulbs hang like dew on a blade of grass, and have preserved the free ends of the brachiophores so that their true length can be seen.

Genus OLIGOMYS Schuchert and Cooper 1931 (Gr. *oligos* = small; *mys* = muscle)

Pl. 1, figs. 4, 8, 15, 17

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 243.

GENOHOLOTYPE.—*Orthis exporrecta* Linnarsson 1876, Bihang till k. svensk. Vet.-Akad. Handl., vol. 3, no. 12, pp. 12-13, pl. 2, figs. 13-19, pl. 3, figs. 20, 21, as illustrated by Walcott (1912, pl. 88, figs. 1-11).

DESCRIPTION. *Exterior.*—Small, transversely oval to subsemicircular, hinge-line straight; cardinal angles usually obtuse; lateral profile very unequally biconvex or plano-convex. Dorsal valve provided with an inconspicuous sulcus best developed at the posterior of the shells and becoming obsolete toward the front; ventral interarea long, curved, strongly apsacline; delthyrium open; dorsal interarea shorter than ventral, moderately anacline; notothyrium open. Surface multicostellate to fascicostellate; costellæ covered by parvicostellæ.

Ventral interior.—Delthyrial cavity deeply sunk, teeth very small, dental plates nearly obsolete; a strong thickening along each margin of the delthyrium serves to strengthen the palintrope and give support to the teeth. Muscle tracks deeply sunk; diductors subtriangular in outline; adductor track linear, widening toward the front and extended forward beyond the ends of the diductors for a short distance; pallial marks consisting of two strong divergent trunks extending forward for more than half the length of the valve.

Dorsal interior.—Brachiophores short, widely divergent, sockets shallow; cardinal process simple, thickened, and widened anteriorly; a strong wide median elevation extends the length of the valve, corresponding to the external sulcus; anterior adductor scars the larger, and separated from the posterior adductors by a thick curved ridge. Diductor scars visible on each side of the cardinal process.

GEOLOGIC RANGE.—Middle Cambrian of Norway and Sweden and Wales. The only species are:

Billingsella exporrecta (Linnarsson) 1876

B. hicksi (Salter MS.) Davidson 1868

B. rugosicostata Walcott 1905

DISCUSSION.—This genus is distinguished from *Billingsella* by the very unequal convexity and external shape of the valves and by its internal structure. According to Walcott, the species here referred to *Oligomys* are provided with a short concave imperforate deltidium "like that of *Conchidium nysius* Hall and Whitfield," extending about one-fifth the length of the delthyrium. If such a structure actually exists it would constitute an important difference between this genus and *Billingsella*, but it was not observed by us; if, however, it is actually present, it must then be compared with the pedicle spoon found in *Protorthis*.

The ventral muscle field of *Oligomys* is small and tripartite as in *Billingsella*; it is usually somewhat elevated on a deposit of adventitious shell at the bottom of the very deep delthyrial cavity. The adductor track is narrow and linear, extended noticeably in front of the diductors, the marks of which are visible on the sides of the dental plates and outside the adductor track. The latter is usually separated from the diductors by narrow longitudinal ridges.

The dental plates are different from those of *Billingsella* in being convergent toward the bottom of the valve. Whether there is an actual union of these

plates on the floor of the valve to form a pedicle spoon, or whether the floor of the delthyrial cavity is covered by a thick deposit of adventitious material between the plates so that the ensemble resembles a pseudospondylium can not be proved definitely in the mature specimens at hand. At any rate, the dental plates are convergent and in this respect are very different from those of *Billingsella*, which are very widely divergent. The difficulty in defining precisely the structure of the dental plates in *Oligomys* is due to the fact that the umbonal cavities are filled with adventitious material at maturity. The ventral pallial trunks are almost exactly like those of *Billingsella* in plan. However, the antero-lateral and antero-median divergence of the main trunk lines is rarely clearly visible.

In the dorsal valve the structure of the cardinalia is essentially the same as that of *Billingsella*, but there are differences in detail. In the first place the dorsal interarea is not so strongly apsacline as in the true *Billingsella*s, with the result that the brachiophores are more inclined. The cardinal process is usually thicker in front and the notothyrial platform is likewise thicker and the axial elevation more prominent. The dorsal musculature is visible clearly in *Oligomys exporrecta*. The anterior adductor scars present an elongate track, but the posterior pair is a small impression outside the plane of each of the anterior adductors. The scars are separated by low oblique ridges in old shells.

Family FINKELNBURGIIDÆ, nov.

(Finkelburgiinae and Orusiinae Schuchert and Cooper 1931)

Primitive, costellate, biconvex Orthacea, having a pseudospondylium and plectorthoid cardinalia.

GEOLOGIC RANGE.—Upper Cambrian to Canadian of the United States, Canada, and western Europe.

Includes but the two genera, *Finkelburgia* and *Orusia*, both of Walcott.

DISCUSSION.—Walcott says⁹ that *Finkelburgia* is derived from *Eoorthis*. The present authors, on the contrary, are inclined to the view that it had its origin in *Orusia* and that it gave rise to *Plectorthis* and the Plectorthidæ. The origin of *Orusia* is unknown.

Genus ORUSIA Walcott 1905

Pl. 1, figs. 2, 7, 9

Walcott, Proc. U. S. Nat. Mus., vol. 28, 1905, p. 273; Camb. Brach., 1912, p. 765, pl. 98, figs. 1-1p, 2-2k, 3-3b, 6-6c.

GENOHOLOTYPE.—*Anomites lenticularis* Wahlenberg 1821, Nova Acta Reg. Soc. Sci. Upsala, vol. 8, pp. 66-67 (transl. in Matthew, Trans. Roy. Soc. Canada for 1891, 1892, vol. 9, sec. 4, no. 5, p. 46).

DESCRIPTION. *Exterior.*—Shell small, subelliptical in outline; hinge-line narrower than the greatest width of the shell; cardinal extremities usually rounded. Lateral profile subequally biconvex; anterior commissure sulcate or rectimarginate, sulcus most strongly marked in the middle and dorsal regions of the shell. Ventral interarea curved, moderately apsacline, delthyrium open. Dorsal interarea shorter than the ventral, anacline. Shell structure unknown.

Ventral interior.—Delthyrial cavity shallow; teeth small, dental plates divergent, sharply defined; muscle area confined; adductor track triangular; diductor tracks narrow, continuous with the pallial marks; pallial trunks widely divergent, as in *Billingsella*.

Dorsal interior.—Notothyrial cavity shallow; brachiophores long and sharp, continuous with sharply defined subparallel plates which extend nearly vertically to the roof of the valve; cardinal process absent.

GEOLOGIC RANGE.—Upper Cambrian to Canadian (according to Bassler 1915).

AMERICAN SPECIES

Orthis lenticularis (Wahlenberg) 1876
O. lenticularis atrypoides Matthew 1892
O. lenticularis lyncioides Matthew 1892
Rafinesquina (?) *atava* (Matthew) 1893
Eoorthis johannensis (Matthew) 1892

EUROPEAN SPECIES

Orthis lenticularis (Wahlenberg)

DISCUSSION.—The genus *Orusia* is made up of small, thin-shelled species characterized by a hinge that is narrower than the width of the valves; sharp, divergent, thin dental plates; and short, discrete, subparallel brachiophore plates that are thin and delicate.

The essential structure of the ventral valve is like that of *Billingsella*, having similar pallial markings and musculature, but is close to *Finkelburgia* in its dental lamellæ. In the dorsal valve, however, the delicacy of the brachiophore plates, together with the fact that the trace of these plates on the internal molds is subparallel, makes them unique among Cambrian brachiopods and relates them to *Finkelburgia*. It has not been possible to determine their exact nature but they extend with a slight curvature to the floor of the valve. The brachiophores, so far as can be observed, are rather long and sharp. The structure of the cardinalia is very close to that of *Finkelburgia*. The musculature of the dorsal valve is not known.

The type of cardinalia in *Orusia* is unique among the known Cambrian orthid brachiopods. In the *Billingsellidæ* and *Nisusiidæ*, support of the brachiophores is accomplished by the swelling of the notothyrial platform laterally and ventrally, so that the plates are buttressed by a foundation of callus. In *Orusia* the advent of discrete plates for the support of the brachio-

⁹ Camb. Brach., p. 320 and table, p. 317.

phores is a great advance over that of other Cambrian forms.

Cummings¹⁰ has suggested the origin of *Platystrophia* from *Orthis lenticularis* (= *Orusia*). There appear to be no anatomical difficulties in the way of this evolution, yet it is impossible to reconcile with this idea the geological position of these genera in time. *Orusia* is an Upper Cambrian and possibly a Canadian genus; *Platystrophia*, on the other hand, is known first from the Trenton in this country. There is thus a vast time gap between the disappearance of *Orusia* and the appearance of *Platystrophia*, a time involving at least all of the Chazyan. The ancestor of *Platystrophia* should be looked for in the Chazyan rather than the Cambrian or Canadian. It appears to us, however, that *Orusia* is ancestral to *Finkelburgia* and perhaps thus directly in the plectorthid line which, as we interpret the facts, gave rise to *Platystrophia*.

Genus FINKELBURGIA Walcott 1905, emended

Pl. 13, figs. 6, 7, 9-19; t. fig. 16

Walcott, Proc. U. S. Nat. Mus., vol. 28, 1905, p. 277; Camb. Brach., 1912, p. 793, pl. 93 (we would select figs. 2 and 2e as representing the genotype).

GENOHOLOTYPE.—*Finkelburgia finkelburgi* Walcott 1905.

DESCRIPTION. *Exterior.*—Subsemicircular to subelliptical; hinge-line straight; cardinal extremities acute or obtuse; lateral profile subequally to unequally biconvex. Anterior commissure rectimarginate. Ventral palintrope longer than the dorsal one, apsacline; delthyrium and notothyrium open, so far as revealed by the specimens studied, but Walcott erroneously states that the delthyrium is partially covered by a deltidium. Surface finely multicostellate. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth strong; dental plates receding; a thickening under the muscles forms a pseudospondylium which is produced into a thick median ridge at the front. Diductor scars divergent, expanding in front; adductor track central, expanded in front, commonly elevated above the diductor scars. Pallial markings two divergent trunks sent off from the anterior ends of the diductors, as in *Billingsella* and *Orusia*.

Dorsal interior.—Notothyrial cavity deep; brachio-phores blunt, fused with supporting plates which converge and unite with the floor of the valve beneath a simple cardinal process where such is present. Sockets defined by flattened plates. Adductor muscles borne on callosities; posterior adductor scars the larger; pallial trunks subradial from the adductor field.

GEOLOGIC RANGE.—Upper Cambrian to Canadian of North America.

SPECIES

Finkelburgia finkelburgi (Walcott) 1905
F. osceola (Walcott) 1905
F. osceola corrugata (Walcott) 1905
Eoorthis newtonensis (Weller) 1903 (in part)
Dalmanella swemplei Cleland 1900
Syntrophia armanda (Billings) 1865

DISTINGUISHING CHARACTERS.—The distinguishing characteristics of *Finkelburgia* are its biconvex lateral profile, finely costellate exterior, and pseudo-spondylium and cardinalia like those of *Plectrothis*.

DISCUSSION.—In the ventral valve the teeth are stout and are located at the angle formed by the hinge and delthyrial margins. The progressive growth of

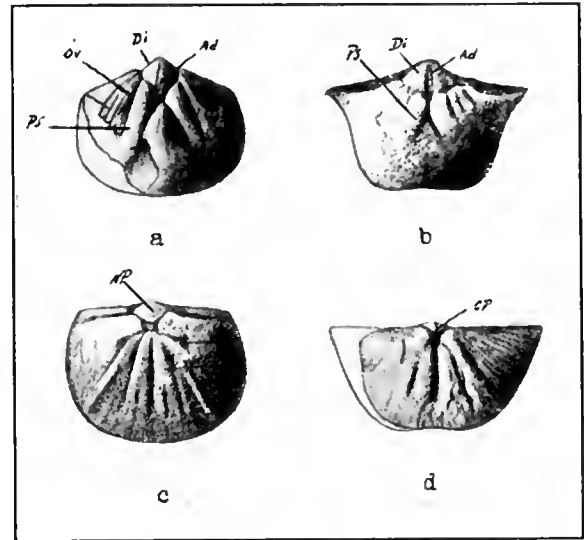


FIG. 16.—a, c, *Finkelburgia osceola* (Walcott). a, ventral internal mold, showing musculature and pallial marks. b, dorsal internal mold. b, d, *F. finkelburgi* (Walcott). b, ventral, and d, dorsal internal mold. After Walcott 1912, pl. 93. NP, notothyrial platform; Ps, pallial sinus; Ov, ovarian markings; Di, diductor scars; Ad, adductor scar; Cp, cardinal process.

the teeth forms a thickening along the margin of the palintrope. The dental plates are attached to the ventral surface along the outer side of this ridge, thus making an overhanging shelf in the delthyrial cavity as in *Skenidioides*. The material forming the pseudospondylium is produced forward in front of the adductor tracks as a low thick elevation to about the middle of the valve. The adductor track is central, expanding slightly in its forward growth. The diductor tracks are divergent, linear. From the anterior end of each diductor track a strong pallial trunk extends anterolaterally. In internal impressions these appear as elevated, divergent ridges. The ensemble of the ventral internal structure is strongly suggestive of some of the *Syntrophiidae*, but differs chiefly in having a pseudospondylium and not a true spondylium.

¹⁰ Amer. Jour. Sci. (4), vol. 15, 1903, p. 6.

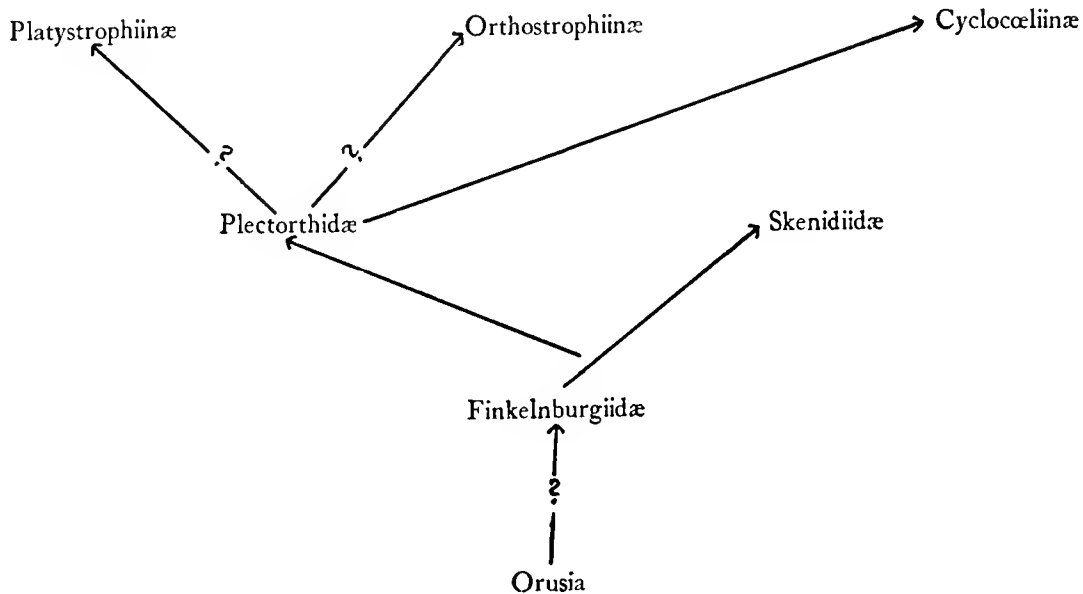
The structure of the dorsal interior of *Finkelburgia* is quite unique among the early brachiopods in the possession of supporting plates attached to the brachio-phores and fulcral plates, forming the sockets as in *Plectorthis*. The cardinal process when present is a simple, linear ridge. It is impossible to say from the material studied whether it bore a crenulated myophore or not. The callosities beneath the adductor scars are another reminder of syntrophiid structure.

Walcott's figures of this genus (pl. 93, figs. 1, 2) are unsatisfactory and verbal corrections are necessary. Figures 1d and 1f, of *F. osceola*, are typical ventral

Family PLECTORTHIDÆ Schuchert and Cooper 1930

The Plectorthidæ are biconvex or convexo-concave Orthacea derived out of the Finkelburgiidae, having a rather variable ventral musculature, but in the dorsal valve a uniform structure of the cardinalia. The brachio-phores are supported by convergent plates uniting with the floor of the valve near the cardinal process. Sockets are defined by small concave fulcral plates. Cardinal process simple, with a compressed crenulated myophore (in the ancestral genus *Finkelburgia*

Table 3



and dorsal valves having the characteristic features of this genus when the two valves are in association. Figure 1e is probably not a *Finkelburgia* since it has a rather strong sulcus, not seen in all the other specimens referred to this genus. Figures 1g and 1h appear to belong to *Eoorthis*.

Figures 2 and 2e of the genotype, *F. finkelburgi*, are taken by us as characteristic of the genus. Figure 2 shows strong pallial markings and a prominent median ridge such as occurs in *F. osceola*. Figure 2e of the dorsal interior shows traces of the musculature and a cardinal process, and displays all the characteristics exhibited by better preserved valves accompanying ventral ones of this species. It is unfortunate that *F. osceola* was not selected as the genotype since well preserved material of this or a closely related form occurs in the Ozarkian (Gasconade) of Missouri. The above description and discussion have been drawn chiefly from two silicified valves of *Finkelburgia*, n. sp., in the U. S. National Museum (see pl. 13, figs. 13, 16, 17, 19), *F. finkelburgi*, and *F. armanda*.

burgia the cardinal ridge when present is devoid of a myophore); it is in the Plectorthidæ that the myophore is seen for the first time. So far as known, the delthyrium and notothyrium are open.

GEOLOGIC RANGE.—Middle Ordovician to close of Silurian.

Divisible into the following subfamilies:

Plectorthinæ Schuchert

Cyclocæliinæ Schuchert and Cooper

Platystrophiinæ Schuchert

? Orthostrophiinæ Schuchert and Cooper

The genetic relations of these various subfamilies appear to be as shown in Table 3.

DISCUSSION.—The Plectorthidæ is one of the most closely knit families in the Orthacea, paralleling the Schizophoriidæ in part of its development. The ventral musculature is rather variable but this may be in large part due to the different external form of some of the genera. In general, however, it may be said that the diductor scars are usually conspicuous, not

enveloping the adductor ones. The individual adductor scars, when visible, are semi-elliptical, forming in the aggregate a lanceolate impression. Usually the adductor scars are not clearly visible, being lodged on the sides of the dental plates or as narrow tracks at their bases. Ventral pallial sinuses usually consist of two abbreviated trunks only, extending from the front of the diductor impressions, except in *Mimella*, which has a very remarkable system of sinuses.

In the dorsal interior the structure is remarkably uniform throughout the family. The cardinal process, with its compressed and crenulated myophore, is uniform except in *Platystrophia*, where it is commonly reduced almost to disappearance. However, the closely related *Mcewanella* has the typical cardinal process of the family.

The divergent brachiophores are moderately long and bluntly pointed. They are supported by sharply defined, convergent plates that unite with the floor of the valve at the cardinal process, forming in some forms a sessile cruralium; in a few specimens the supporting plates actually unite with a median septum but this is rare.

In this family as elsewhere the mantle deposits extra testaceous shell over the whole internal surface. This tendency is particularly noticeable in *Platystrophia*, and it has been carried so far in the average forms of this genus as to obscure the actual morphology completely and cloud the genetic relationships. In the ventral valve the dental plates are obliterated by deposition in the umbonal cavities, and in the dorsal valve the fulcral plates may be lost from view by filling of the cavity between that plate and the brachiophore support.

The Plectorthidæ form a homœomorphic series with *Schizophoria* of the Schizophoriidæ. *Schizophorella* and *Mimella* of the former group represent the biconvex or lenticular phase in the evolution, corresponding to *Pionodema* of the Schizophoriidæ, while *Hebertella* is the advanced or convexo-concave stage comparing well with *Schizophoria*. The evolution of the Hebertellas is far more accelerated than that of the impunctate group. The former are last seen in the Upper Ordovician of North America, but *Schizophoria* persists into Upper Pennsylvanian time.

Subfamily PLECTORTHINÆ Schuchert 1929, emended

Coarse- and fine-ribbed Plectorthidæ having wide hinge-lines and unequal interareas.

DISCUSSION.—In emending this subfamily it is found necessary to exclude from this association *Eridorthis* and *Cyclocarlia*. On a later page we have shown that the former, by its internal structure, belongs to the Glyptorthinæ of the Orthidæ; and *Cyclocarlia* is aberrant in form and placed by us in a separate subfamily.

On the other hand, we have transferred to the Plectorthinæ the genera *Hebertella* and *Schizophorella*. As now constituted, therefore, the Plectorthinæ form the largest subfamily of the Plectorthidæ, including the following genera:

Plectorthis Hall and Clarke
Hebertella Hall and Clarke
Mimella Cooper
Schizophorella Reed
Doleroides Cooper

The genetic relationships are thought to be as shown in Table 4.

Genus PLECTORTHIS Hall and Clarke 1892

Pl. 11, figs. 1-5, 9, 15

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, pp. 194, 221, pl. 5, figs. 18-20.

GENOTYPE.—*Orthis plicatella* Hall 1847, Pal. N. Y., vol. 1, p. 122, pl. 32, fig. 9.

DESCRIPTION. *Exterior*.—Transversely semielliptical, anterior and lateral margins convex; lateral profile lenticular, uncommonly with the ventral valve concave at the front; anterior commissure faintly sulcate or uniplicate; interarea of the ventral valve strongly apsacline; slightly curved, comparatively short; dorsal interarea orthocline or faintly anacline, shorter than the ventral interarea, slightly curved; delthyrium and notothyrium unmodified; ornamentation paucicostate to multicostate, interspaces marked by fine elevated lines of growth. Test thin, fibrous, impunctate.

Ventral interior.—Delthyrial cavity shallow, umbonal cavities deep, teeth small, situated on the apex formed by the hinge- and delthyrial margins; crural fossettes oblique, faintly defined; dental plates thin, clearly defined, advancing, continued as a slight thickening for some distance around the lateral margins of the diductors. Muscle area heart-shaped, occupying between one-third and one-half the length of the shell; adductor track linear, confined within the diductor scars; diductors subrescentic; a low ridge extends forward for a short distance from the adductor track in some specimens; anterior margin and whole interior multicostate.

Dorsal interior.—Notothyrial cavity shallow; cardinalia confined to about one-fifth the length of the shell; brachiophores short, stout, grooved inside, forming the margin of the notothyrium and supported by thin plates that converge and unite with the floor of the valve beneath the cardinal process. Sockets deep, excavated beneath the palintrope, defined by a small fulcral plate. The brachiophore supports in old shells are commonly obliterated by the deposition of adventitious shell in the lateral cavities. Cardinal process a thick, rounded ridge, having a crenulated myophore. In old shells a short median ridge extends from the anterior

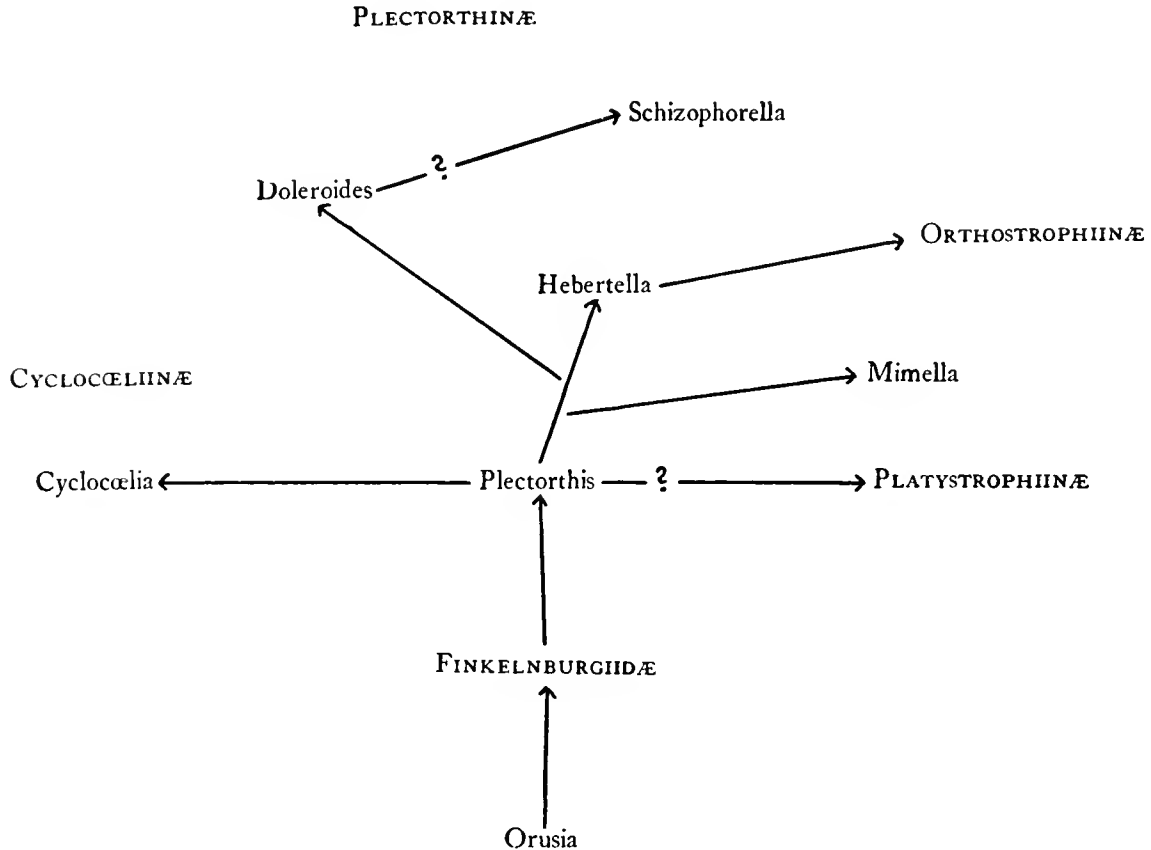
margin of the notothyrial platform. The dorsal musculature has not been observed.

GEOLOGIC RANGE.—Middle and Upper Ordovician (Chazy? to Maysville) of North America.

name, but their analysis of the group is inadequate. They define *Plectorthis* as follows (pp. 194, 195):

While it retains the strong external ribs of the typical *Orthis*, these are not invariably simple (*O. fissicosta*, Hall;

Table 4



AMERICAN SPECIES

- Plectorthis æquivalvis* (Hall) 1847
P. æquivalvis latior Foerste 1910
P. æquivalvis pervagata Foerste 1910
P. fissicosta (Hall) 1847
P. jamesi (Hall) 1861
P. neglecta (James) 1879
P. plicatella (Hall) 1847
P. plicatella trentonensis Foerste 1910
P. ? sinuatis Wilson 1926
P. triplicatella (Meek) 1872
? P. holdeni Willard 1928
? P. exfoliata (Raymond) 1905

EUROPEAN SPECIES

- ? Orthis scotica* McCoy

DISCUSSION.—Hall and Clarke recognized the uniqueness of the group of shells characterized by *Orthis plicatella* Hall by giving this division a separate

O. triplicatella, Meek; *O. æquivalvis*, Hall, not Davidson; *O. Jamesi*, Hall); the cardinal area of the pedicle-valve is comparatively low and the valves are subequally convex. In the interior the character of the muscular scars, dental lamellæ and cardinal process is essentially the same as in Group I [= *Hesperorthis*], and the minute structure of the shell seems to be in precise agreement with that of *O. calligramma* [= *Orthis s. s.*], though no evidence of tubulose costæ has been observed. In *Orthis Jamesi*, which is placed in this association, there is occasionally a deviation toward the resupinate contour exemplified in the Groups IV and V [= *Plasiomys* and *Hebertella*].

In defining this group Hall and Clarke evidently had in mind its variations from their *Orthis s. s.*, which was based chiefly on *Orthis tricenaria* [= our *Hesperorthis*]. The interareas are rather different from those of *Hesperorthis* but do actually resemble those of *Orthis s. s.* as here defined in the rather prominent incurvature of the ventral interarea. Hall and Clarke err when they state that "in the interior the character of

the muscular scars, dental lamellæ and cardinal process is essentially the same as in Group I *Orthis* [= *Hesperorthis*]." This statement has led to the popular conception that *Plectorthis* is a biconvex orthid with a low cardinal area, having the internal structure of their *Orthis s. s.* (*Hesperorthis*). Let us therefore examine into the detailed internal anatomy of this genus, taking up the various structures in the order named by Hall and Clarke.

The ventral muscle plan when examined in detail is admittedly close to that seen in *Orthis s. s.* but is also equally close to that of *Hebertella*. Resemblances to *Orthis s. s.* are to be seen in the subrescendent diductor scars and the linear adductor track. However, this difference is to be noted, that the diductor scars are more expanded in front, exactly as those of *Hebertella*, and the adductor track is double-ridged as in the latter genus.

Although the ventral musculature is similar to that of *Orthis s. s.*, the dental lamellæ, cardinalia, and pallial markings are so different as to set apart *Plectorthis* from the Orthidæ. The dental plates are thin septa forming the walls of the delthyrial cavity. They also bound deep lateral umbonal cavities. These lamellæ extend directly to the floor of the valve. The teeth that they buttress are located at the angle between the delthyrial and the hinge margin. In the Orthidæ the teeth are usually situate laterally of the delthyrial margins. *Plectorthis* does not have the reniform ovarian impressions characteristic of *Orthis* and lacks also the elongate median ridge which divides the two pallial trunks extending forward from the anterior ends of the diductor scars. *Plectorthis* has a slight median ridge extending forward from the adductor track but it occupies a distance of one or two millimeters only. Accordingly, the aggregate of ventral internal features and the absence of certain pallial and ovarian markings universal in the Orthidæ relate the ventral shell of *Plectorthis* to *Hebertella* rather than to *Orthis s. s.*

When the structures of the dorsal valve of *Plectorthis* are studied, the true relationship of the genus to *Hebertella* and to *Platystrophia* becomes apparent. The chief resemblance between these genera and *Plectorthis* lies in the character of the cardinalia and it is here also that the most fundamental distinction between *Orthis s. s.* and *Plectorthis* is to be found. The brachio-phores of the latter are blunt plates intimately united with thin, supporting plates which converge toward each other and unite with the floor of the valve beneath the cardinal process. This type of cardinalia occurs also in the genera *Mimella*, *Hebertella*, and *Doleroides*, all members of the Plectorthinæ. *Plectorthis* is further characterized by the presence of a small concave plate, the fulcral plate, attached to the brachio-phore and to the inner wall of the valve. This plate defines the rather deep socket and serves to strengthen the union of the brachio-phores and their supporting plates to the walls of the valves. This structure is in marked con-

trast to that of *Orthis s. s.* in which the brachio-phores are simple rodlike elements supported by the swelling of adventitious shell deposited on the notothyrial platform and walls of the valve.

Hall and Clarke found further resemblance in the cardinal processes of *Plectorthis* and *Orthis s. s.* In the latter this process is always a simple ridge, not uncommonly bladelike in appearance. It is difficult to find scars of muscle attachment on such a ridge but they have been seen on its sides and at its base. The cardinal process of *Plectorthis*, however, is like that of *Dinorthis* in having a stout compressed shaft, which bears a crenulated myophore. The crenulation may be on the posterior surface but is usually impressed on the sides of the process, forming an excavation on each side and thus narrowing the posterior part of the structure. This type of cardinal process also characterizes *Hebertella* and makes the resemblance to that genus all the more striking.

Another minor point of difference between *Orthis s. s.* and *Plectorthis* is to be found in the interlocking of the valves along the front and lateral margins. In the Orthidæ as described on an earlier page the spaces between the ribs on the outside correspond to double ridges on the inside, but in *Plectorthis* the interspaces form simple rounded costellæ on the inside of the front margin.

In North America *Plectorthis* is known with certainty in the early Trenton limestone and ranges through the Mohawkian into the Richmond of the Upper Ordovician. Two species from the Chazy, *Hebertella exfoliata* Raymond and *Plectorthis holdeni* Willard, have been doubtfully referred to this genus, but in neither form as yet has the interior been seen.

Plectorthis is not known certainly in Europe. From examination of the figures of several species referred to *Plectorthis* in Cowper Reed's work on the Girvan district, the writers would not admit a single one into the genus as here defined. However, *Hebertella scotica* (McCoy) has the external characteristics of *Plectorthis* and Reed's figures of the dorsal interior show structures similar to those in this genus. The other species referred to *Plectorthis* are to be distributed among the genera *Orthis s. s.*, *Schizorammina*, and *Dolerorthis*.

Plectorthis did not survive into the Silurian. It may have originated in the Chazy, but more probably in the Canadian, and apparently arose out of *Finkelnburgia*, which has cardinalia that could readily have evolved into those of *Plectorthis* (see p. 56).

Genus HEBERTELLA Hall and Clarke 1892

Pl. 11, figs. 14, 17, 19-26

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, pp. 198, 222, pl. 5a, figs. 1-10.

GENOTYPE.—*Orthis sinuata* Hall 1847, Pal. N. Y., vol. 1, p. 128, pl. 32B, fig. 2.

DESCRIPTION. *Exterior.*—Shells large or small, subelliptical or subquadrate; hinge-line straight, usually narrower than the greatest width; cardinal extremities rounded or angular, occasionally deflected; lateral profile convexo-concave or unequally biconvex; anterior commissure uniplicate, uncommonly sulcate; anterior margins rarely emarginate. Ventral palintrope generally strongly apsacline, slightly curved; dorsal palintrope shorter than the ventral, orthocline or apsacline, curved; ventral beak slightly incurved; dorsal beak arched over the ventral interarea, umbogently convex or inflated; exterior paucicostate to multicostate with fine concentric ornamentation; swollen tubulose costæ. Test fibrous, internally impunctate, scattered exopunctæ on the surface.

Ventral interior.—Delthyrial cavity deep; teeth strong, with lateral sockets, crural fossettes oblique, moderately deep; dental plates strong; umbonal cavities deep, muscle field obcordate, strongly impressed, bounded by an elevated ridge extending from the anterior ends of the dental plates; diductor scars subcrescentic, not enclosing the adductor track in front; adductor scars elongate suboval, borne on a double median ridge which has a shallow groove in the center; adjustor scars obscure at the base and on the sides of the dental plates; pedicle callist visible in some shells, small, slightly elevated above the floor; ovarian markings consisting of interrupted wavy elevated lines, most prominent on each side of the muscle field.

Dorsal interior.—Notothyrial cavity deep, brachio-phores marginating notothyrium, divergent, bluntly pointed, supported by convergent plates which unite with the roof of the valve; socket deep, marked by a small fulcral plate; cardinal process a thick ridge, median thickening extending to the center of the valve; muscle marks obscure, posterior pair larger than the anterior ones; pallial markings a few oblique, radial lines from the crural cavities.

GEOLOGIC RANGE.—Middle and Upper Ordovician (Chazy? to Richmond) of North America.

SPECIES

- Hebertella alveata* Foerste 1909
H. alveata richmondensis Foerste 1909
H. frankfortensis Foerste 1909
H. latasulcata Foerste 1914
H. maria (Billings) 1862
H. maria parkensis Foerste 1909
H. occidentalis (Hall) 1847
H. occidentalis sinuata (Hall) 1847
H. subjugata (Hall) 1847
H. clermontensis Bradley 1921
 (looks like *Dinorthis proavita*)
 ? *H. louensis* (Walcott) 1884

DISTINGUISHING CHARACTERS.—*Hebertella* is characterized externally especially by the convexo-concave or unequally biconvex profile of the valves and the

multicostellate ornamentation. Internally the plan of the ventral muscle field with the double adductor ridge is unique. In the dorsal valve the cardinalia are as in *Plectorthis*.

DISCUSSION.—The ventral muscle field is characterized by wide diductor scars having thickened inner margins which form a double central ridge. Upon this ridge are located the adductor muscles, forming together an elongate oval scar. The adjustor marks are located on the sides of the dental lamellæ, where they join the valve and usually escape notice. The other margins of the muscle area are commonly elevated strongly, forming a deep basin. In old shells a callus is deposited at the back end of the shell, obliterating all the muscle impressions in its growth forward (see pl. 11, fig. 24). In the apex is a rather small pedicle callist, commonly elevated slightly above the floor of the valve. In some instances it is so small as to be of doubtful value in the attachment of the pedicle. Not uncommonly a double-ridged median elevation develops from the anterior end of the callist and grows forward, in some instances for half the length of the muscle field. It is a common phenomenon of *H. occidentalis sinuata* to see one or two slight median ridges extending for a short distance in front of the median double muscle track. It is a striking fact that *Hebertella* shows no conspicuous pallial markings except an irregular pitting of the surface, and, in the vicinity of the umbonal cavities, interrupted, elevated lines or ridges.

The dorsal interior is essentially the same as that of *Plectorthis*. In old shells the cardinal process may become bulbous in front but the myophore remains a thin, bladelike ridge crenulated on its sides. The posterior adductor impressions are the larger and in old age are longitudinally ribbed. As alluded to previously, *Hebertella* and *Plectorthis* are very closely related. Young forms of *Hebertella* can scarcely be distinguished from some mature species of *Plectorthis*, either externally or internally (see pl. 11). This genus may or may not be the ancestor of *Hebertella*; it is impossible to determine this until the Chazy "*Plectorthis*" are more seriously investigated. However, the two lines have a common origin and certainly belong in the same family, but each genus may have arisen independently out of *Finkelburgia*.

As conceived by Hall and Clarke, the genus *Hebertella* comprised a heterogeneous assemblage of shells including such genera as *Glyptorthis*, *Eridorthis*, and *Austinella*. It has already been shown that *Glyptorthis* and *Eridorthis* are wholly unrelated to *Hebertella* and belong in a different family.

Hebertella appears to be confined to the Ordovician of North America. Reed has referred certain Girvan shells to this genus but none of them agree with *Hebertella*. The species *H. balclatchiensis* and *H. crispa* appear to belong to *Glyptorthis* and consequently are of a

different family. *H. bellatrix* Reed¹¹ has the cardinalia characteristic of *Orthis s. s.* and *Hesperorthis*, and *H. lapworthi* must be referred to *Ptychopleurella*. Foerste has referred to *Hebertella* a dorsal valve identified by Salter as *Orthis retrorsa*, calling it *H. llaniloensis*, but since only the exterior was seen by Foerste its reference to *Hebertella* is very doubtful.¹² It is therefore remarkable, when one considers the wide distribution and abundance of *Hebertella* in North America, that there should be in Europe no representatives of the *O. sinuata* type.

Genus MIMELLA Cooper 1930

Pl. 12, figs. 5, 6, 8, 10, 14, 15, 20; t. fig. 6

Cooper. Jour. Pal., vol. 4, 1930, pp. 375, 382, pl. 35, figs. 9-12, 15.

GENOHOLOTYPE. — *Pionodema globosa* Willard 1928, Bull. Mus. Comp. Zool., vol. 68, p. 274, pl. 2, fig. 5.

DESCRIPTION. *Exterior*.—Externally like *Pionodema* of the Schizophoriidae, transversely subelliptical; margins rounded; cardinal extremities obtuse; hinge-line straight; lateral profile subequally biconvex, the dorsal valve usually the more so; anterior commissure uniplicate; a slight sulcus developed on the ventral valve only at the front of the shell. Ventral inter-area long, curved, strongly apsacline; umbo strongly convex, beak curved, delthyrium open. Dorsal inter-area shorter than the ventral, faintly apsacline, umbo very convex. Ornamentation multicostellate, elevated growth-lines undulating over the whole surface. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth small; fossettes shallow; dental plates prominent, receding, continued around the lateral margins of the diductor scars as a low ridge; umbonal cavities deep; muscular area large, trilobate; diductor scars divergent, narrow, linear, not noticeably expanded in front; adductor track linear, expanding toward the front, occupying a strongly elevated track between the diductor scars; adjustor scars obscure; pedicle callist small, slightly elevated. Pallial markings prominent, consisting of a wide trunk extending antero-laterally from the anterior ends of the diductor scars. This trunk bifurcates and sends a subsidiary one postero-laterally and another antero-medially. Both of these split repeatedly into minor distributaries. The antero-median curving of the two trunks noted above produced a heart- or shield-shaped area occupied by elongated

papillae in front of the muscle field. Such papillae occupy all of the spaces not covered by pallial marks.

Dorsal interior.—Notothyrial cavity deep, brachio-phores not separable from their supporting plates. The latter converge toward each other to unite with a median ridge, forming thereby a sessile cruralium. In young adults there are marked cavities beneath the brachio-phore supports but in old forms these are filled with adventitious shell. The sockets are shallow and are defined by a fulcral plate. Cardinal process a thin linear ridge. The median ridge is thin and subcarinate and extends for about one-half the length of the shell. Adductor scars subequal.

GEOLOGIC RANGE.—Middle Ordovician (Chazy) of North America.

SPECIES

Pionodema globosa Willard 1928

P. minuscula Willard 1928

Hebertella melonica Willard 1928

? *H. vulgaris* Raymond 1906

? *H. imperator* (Billings) 1859

DISTINGUISHING CHARACTERS.—The various species of *Mimella* show a convergence toward the external form of *Pionodema* as striking as the homœomorphy of *Doleroides* and *Pionodema*.¹³ The genus is characterized chiefly by its remarkable pallial markings, trilobed ventral muscle field, and a dorsal interior having the features of *Hebertella*.

DISCUSSION.—*Mimella* is closely related to *Hebertella* in the structure of the dorsal valve. The chief distinction between the two seems to be in the delicacy of the parts rather than in their general arrangement, and this delicacy appears to be due to the earlier appearance of *Mimella*. The cruralium is usually deeper and more U-shaped in *Mimella* and the cardinal process and median ridge are thinner. The cardinal process, however, is of the plectorthoid type. The median ridge is a rather high but thin partition, while in *Hebertella* it is low and wide.

The diagnostic feature of *Mimella*, as said above, is the arrangement of the ventral pallial markings, and it is the only genus of the Plectorthidae that has them well developed, a feature in common with many of the forms of *Dinorthis* (*Plasiomys*). They differ chiefly in that the postero-lateral branch of the main trunk, so well developed in *Plasiomys*, is sent off nearly directly laterally in *Mimella*. This is probably due to the fact that the muscles are more confined to the back part of the valve in *Mimella*. Furthermore, the subsidiary rami of the tertiary branches are less numerous than in *Dinorthis* (*Plasiomys*).

¹¹ Left unplaced.

¹² The junior author has since seen plastotypes of *Hebertella llaniloensis* in the U. S. National Museum and is convinced that the specimens are dorsal valves belonging to *Dinorthis* (*Retrorsirostra*).

¹³ See Cooper, Jour. Pal., vol. 4, no. 4, 1930, pp. 369-382.

Hebertella vulgaris Raymond and *Orthis imperator* Billings are tentatively placed under *Mimella*. Both species have the divergent diductor scars, the narrow median ridge, and the thin cardinal process characteristic of that genus. However, the typical pallial markings were not observed. The ventral musculature of both species differs considerably from that of *Orthis sinuata* Hall.

Many specimens of *Mimella* have been referred to *Pionodema* in the past. Their external form is clearly that of this genus but the impunctate nature of the test, the trilobate ventral musculature, and the cruralium should serve to differentiate the two genera.

Genus SCHIZOPHORELLA Reed 1917

Pl. 12, figs. 1-4, 7, 9

Reed, Trans. Roy. Soc. Edinburgh, vol. 51, pt. 4, 1917, p. 858, pl. 10, figs. 19-24.

Cooper, Jour. Pal., vol. 4, 1930, p. 377, pl. 36, figs. 10, 12, 13, 15.

GENOHOLOTYPE.—*Orthis fallax* Salter 1846, Synop. Sil. Foss. Ireland, Add., p. 72, pl. 5, fig. 3.

DESCRIPTION. *Exterior*.—Semicircular to subelliptical; margins and cardinal angles rounded or obtusely angular; unequally biconvex, with the dorsal valve usually the more convex; hinge-line straight, narrower than the greatest width of the shell. Anterior commissure uniplicate, fold and sulcus developed best in front of the middle of the shell. Ventral interarea longer than the dorsal, plane or slightly curved, strongly apsacline; ventral umbo convex, beak incurved. Dorsal interarea slightly curved or plane, faintly apsacline to faintly anacline; umbo strongly convex, beak scarcely defined. Delthyrium open; notothyrium closed by the cardinal process. Ornamentation multicostellate; test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth strong, with oblique crural fossettes. Dental plates strong, continued as a ridge around the margins of the diductor scars and nearly uniting in front. Umbonal cavities deep. Muscle area subelliptical, occupying more than one-third the length of the valve. Diductor scars elongate, enclosing a lanceolate adductor field; adductor scars hemi-elliptical, divided centrally by a ridge which separates the front ends of the diductor scars and is continued forward for a considerable distance toward the front margin. Adjustor scars small and obscure. Umbo-lateral spaces occupied by strongly marked radial ridges which indicate the position of the ovarian bodies.

Dorsal interior.—Notothyrial cavity moderately deep; cardinalia confined; sockets defined by a fulcral plate; brachiophores strong, curved slightly, with their supporting plates extended to the floor of the valve; cardinal process plectorthoid. Adductor scars

unequal in size, the posterior pair being the larger, separated by low curved ridges extending antero-laterally from the median ridge. Internal surface marked by oblique elongate ovarian ridges.

GEOLOGIC RANGE.—Upper Ordovician (Drummock group) of the British Isles. The only species known to the writers is the genotype, *O. fallax* Salter.

DISTINGUISHING CHARACTERS.—This genus is most easily distinguished by its pionodemoid outline and profile, hebertelloid dorsal interior, and the ventral muscle field which has a number of variations from the pattern usually seen in *Hebertella*.

DISCUSSION.—Through the kindness of the British Museum we have been able to study specimens of the genotype and of *S. mullochensis* (Davidson), a Silurian species that Reed referred to this genus. From our studies it is apparent that the two species show a remarkable instance of heterochronous homœomorphy, since the Ordovician *S. fallax* has an impunctate shell and the Silurian form a punctate one. The specimens studied have the following catalogue numbers: *S. fallax*, B 52118, B 52121-41; *S. mullochensis*, B 44590-96, B 44607-10, and B 44615-16. Fortunately specimens B 52136 and B 52118 of *S. fallax* and B 44607-10 and B 44590-96 of *S. mullochensis* retain some of the original shell substance adhering to the internal molds. This happy circumstance led us to see the punctate test and accordingly to remove *S. mullochensis* from association in this genus, referring it to the new genus *Mendacella* Cooper proposed in 1930 and discussed later in this work.

Since *Schizophorella* now proves to have an impunctate shell, the name chosen by Reed is unfortunate, inasmuch as it implies relationship with the genus *Schizophoria*. The genus under discussion, however, clearly belongs in the Plectorthidæ and in close association with *Hebertella*.

Hebertelloid characteristics are seen in *Schizophorella* in the plan of the ventral muscle field and the nature of the cardinalia. The diductor impressions have the general form seen in *Hebertella*, being somewhat expanded in front, thickened on the outer margins, and enveloping tightly the adductor impressions. The latter are implanted on a low ridge, forming together a narrow elliptical or lanceolate scar. The median ridge is usually extended forward as a low elevation nearly to the front of the valve. The dorsal musculature, cardinal process, brachiophores and their supporting plates are exactly like those of *Hebertella*, and the sockets are defined by concave socket plates. Some of the specimens of *Schizophorella* show the brachiophore supports separated at their junction with the valve, but this is a perfectly normal condition in young shells throughout the Plectorthidæ.

Reed's genus is close to the American *Doleroides* but differs in certain important details. The British genus also appears later on the geological horizon.

Genus **DOLEROIDES** Cooper 1930

Pl. 11, figs. 6-8, 10-13, 16, 18

Cooper, Jour. Pal., vol. 4, 1930, pp. 375, 382, pl. 35, figs. 5-7, 14; pl. 37, fig. 2. Also *D. pervetus*, p. 381, pl. 35, fig. 8; pl. 36, figs. 4, 7; pl. 37, figs. 1, 3, 13.

GENOHOLOTYPE.—*Orthis gibbosa* Billings 1857, Geol. Surv. Canada, Rept. Progress for 1856, p. 296.

DESCRIPTION. *Exterior.*—Externally *Doleroides* corresponds closely to *Pionodema*, being lenticular or nearly so in profile and subsemielliptical in outline. The ventral interarea is the longer, the delthyrium is open, and the notothyrium is modified only by the cardinal process. The surface of the shell is multicostellate, with numerous hollow costellæ; test fibrous, impunctate.

Ventral interior.—Dental lamellæ prominent; diductor impressions subcrescentic, elongate, surrounded on the outside by a thickened margin; adductor ridge single; adductor field elliptical; adjustor impressions elongate, narrow. Umbo-lateral spaces marked by radial ovarian ridges. The entire inner surface of the shell is marked by low radial ridges and elongate pustules.

Dorsal interior.—The cardinal process is a thick ridge with a plectorthoid myophore, long blunt brachio-phores with convergent supporting plates forming a shallow sessile cruralium. Concave fulcral plates unite the brachio-phores to the walls of the valve and define the sockets. Umbo-lateral spaces marked by interrupted, wavy, radial ridges.

GEOLOGIC RANGE.—Lower Middle Ordovician (Black River) of North America.

SPECIES

Dalmanella subæquata gibbosa (Billings) 1857

D. subæquata perveta (Conrad) 1843

Undescribed species

DISCUSSION.—It is evident from the internal features of this genus that it is very closely related to *Hebertella*, differing chiefly in its subequal biconvexity and ventral musculature. The latter differs from that of *Hebertella* chiefly in lacking the double median adductor ridge and in having the adjustor impressions more strongly developed. The dorsal interior is identical with that of *Hebertella*.

This small group of plectorthids forms a remarkable example of homæomorphy. So precise is the mimicry of *Pionodema* by *D. gibbosa* that this species has usually been identified as "*Pionodema subæquata gibbosa* (Billings)." The occurrence of these shells side by side (isochronous homæomorphy) further militates against their accurate identification. The mimicry is

carried so far that *Doleroides* even has an abundance of hollow costellæ, although they are not quite so numerous as in *Pionodema*.

The chief external distinguishing features between *Doleroides* and *Pionodema* are the almost uniformly wider hinge-line, the more pronounced and more universal fold and sulcus, and the less abundant hollow costellæ in the former. Further, the costellæ in *Doleroides* are in general coarser than those of *Pionodema* in shells of about the same size. Internally, however, the separation of the two is easy. In the ventral valve of *Pionodema* there is a small apical plate, the diductor impressions are subflabellate, and the adductor ridge is extended in front of the anterior margin of the muscle field. In *Doleroides*, on the other hand, there is no apical plate, the muscle field is bounded by an elevated border, and the adductor ridge is confined to the muscle field (compare fig. 6, pl. 11 with fig. 9, pl. 23). In the dorsal valve the brachio-phore supports of *Pionodema* are divergent, not convergent as in *Doleroides* (compare fig. 12, pl. 11 with figs. 7, 8, pl. 23). The final and most conclusive test of generic dissimilarity between these homæomorphs is, of course, a thin section of the shell, *Pionodema* being punctate.

In general appearance, *Doleroides* is similar to *Schizophorella* of Europe, but there are important differences. Externally the American shells do not have the strong development of the fold and sulcus characteristic of the European species. *D. gibbosus* shows a rather prominent fold and sulcus but in *D. pervetus*, as understood, the dorsal valve is provided with a sulcus in young stages which is lost later on at the front of the valve. In some specimens, however, there is a distinct dorsal fold in the mature shells, and in rare instances a sulcus may be present on both valves, producing an emargination of the anterior margin. They thus show the same instability of fold and sulcus exhibited by *Hebertella* and other more primitive genera of brachiopods.

Internally the variation of *Schizophorella* from *Doleroides* is more pronounced. In the ventral valve of some specimens the adductor ridge is continued forward beyond the confines of the adductor field nearly to the front margin of the shell, and in the dorsal valve the brachio-phore supports are always convergent but may remain discrete at their union with the floor of the valve. This condition may also be observed in the young of *Plectorthis*, in which these plates either unite with the floor and remain slightly separated, or unite with each other and with the floor of the valve simultaneously. In *Schizophorella* both conditions occur in the same species. If we add to these differences a later geological age and a different geographical province, we see at once the full significance of these small variations. *Doleroides* is chiefly at home in Middle Ordovician (Black River) rocks of North America, whereas *Schizophorella* occurs in the Upper Ordovician of the British Isles.

Subfamily CYCLOCÆLIINÆ Schuchert and
Cooper 1931

Plectorthidæ which probably originated in the Plectorthinæ, and in which the hinge-line and cardinal areas are so narrowed as to produce a rostrate shell suggestive of the rhynchonellids.

The subfamily embraces but the one genus, *Cyclocælia*, restricted to the Upper Ordovician of the Ohio Valley.

Genus CYCLOCÆLIA Foerste 1909

(*Encyclodema* Foerste 1912)¹⁴

Pl. 10, figs. 1-5, 7, 9

Foerste, Bull. Sci. Lab. Denison Univ., vol. 14, 1909, p. 227; vol. 16, 1910, p. 36, pl. 2, fig. 10, pl. 6, figs. 8a, b.

GENOHOLOTYPE.—*Atrypa sordida* Hall, 1847, Pal. N. Y., vol. 1, p. 148, pl. 33, fig. 16.

DESCRIPTION. *Exterior*.—Shell small, rhynchonelliform to subcircular, anterior and lateral margins convex, hinge-line very narrow; lateral profile biconvex, lateral commissure unflexed; anterior commissure rectimarginate to faintly uniplicate; interarea of the ventral valve narrowly triangular, apsacline; beak subrostrate, delthyrium open, umbo convex; dorsal interarea very short, apsacline, umbo very convex. Ornamentation pauci- to multicostate. Test very thin, impunctate.

Ventral interior.—Delthyrial cavity moderately deep; teeth strong; dental plates sharply defined, strong, diverging, extending nearly one-fourth the length of the shell; muscle area not impressed on the thin shell.

Dorsal interior.—Cardinalia confined, like those of *Plectorthis*; brachioophores diverging, "rather broad," and terminating "anteriorly [ventrally] in a point" (Foerste), supported by curved plates uniting with the median ridge on the floor of the valve; cardinal process an obscure ridge; median septum extending anteriorly about one-fourth the length of the valve. Adductor scars not impressed on the shell.

GEOLOGIC RANGE.—Early Upper Ordovician of the Ohio Valley.

SPECIES

Plectorthis crassiplicata (Foerste) 1910

P. sectistriata (Ulrich) 1879

P. sordida multiplicata (Foerste) 1910

Rhynchonella sordida Hall 1847 (syn. *Orthis ella*)

¹⁴ Schuchert and LeVene in 1929 followed Foerste in regarding *Cyclocælia* as a homonym. However, it appears that, according to the rules, it is not preoccupied by *Cyclocæla* Duf. 1839, as Foerste supposed, and hence the original name given by the latter in 1909 should stand.

DISCUSSION.—*Cyclocælia* forms a compact group of small rhynchonelloid shells having essentially the internal characters of *Plectorthis*. The author of the genus published only a short analysis of the internal features. The presence of interareas on both valves, the open delthyrium of the ventral valve, and the plectorthoid interior show that the genus is not a rhynchonellid. It differs from *Plectorthis* mainly in the narrowness of the hinge-line, which has produced the subrostrate condition of the ventral valve. It agrees with that genus in the strength and character of the dental plates and in having the same type of cardinalia, but the cardinal process is much reduced and the whole apparatus more abbreviated. The shell is too thin to have preserved any trace of the muscular impressions.

The rhynchonelloid form consequent on the narrowing of the hinge-line is therefore the fundamental basis of distinction of this group from *Plectorthis*. The presence of three species and one variety in the genus shows the definiteness of the evolution toward the rhynchonelloid form and is a favorable argument for giving these shells a separate designation. It is obvious that *Cyclocælia* is a deviation from the *Plectorthis* line.

The development of such a rhynchonelliform shell as *Cyclocælia*, and the several independent reappearances of this form in orthid shells, suggest the probability that the Rhynchonellacea may have originated in the Orthacea, but not in *Cyclocælia*, since that genus appeared long after true rhynchonellids had arisen.

Another rhynchonelliform orthid is the Russian genus *Angusticardinia*, but this has a different ancestry from *Cyclocælia*; moreover, the former has orthoid cardinalia, while those of *Cyclocælia* are plectorthoid.

Subfamily PLATYSTROPHIINÆ Schuchert 1929

Biconvex, coarsely costate Plectorthidæ which either arose in *Plectorthis*, or came out of the *Finkelburgia* stock. With large subequal interareas, prominent fold and sulcus, and usually a spiriferoid outline.

GEOLOGIC RANGE.—Middle Ordovician to close of Silurian in the northern hemisphere.

Includes but two genera, *Platystrophia* King and *McEwanella* Foerste.

Genus PLATYSTROPHIA King 1850

Pl. 12, figs. 13, 16, 19, 23-27

King, Mon. Perm. Foss., 1850, p. 106.

Davidson, Brit. Foss. Brach., vol. 1, Introd., 1851-1855, p. 103.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, p. 200, pl. 5B, figs. 1-10.

Cumings, Amer. Jour. Sci. (4), vol. 15, 1903, pp. 1-48, 121-136.

McEwan, U. S. Nat. Mus., Proc., vol. 56, 1919, pp. 383-448.

GENOHOLOTYPE.—*Terebratulites biforatus* Schlotheim 1820, Petref., p. 265.

DESCRIPTION. *Exterior.*—Shells spiriferoid, anterior margin truncate, emarginate, or lobate; hinge-line straight, commonly mucronate; cardinal angles acute or obtuse; lateral profile strongly biconvex, commonly globular; anterior commissure strongly uniplicate; umbos inflated, palintropes very broadly triangular, curved, subequal, beaks incurved, ventral area vertically striate, ventral beak commonly resorbed by the pedicle; delthyrium and notothyrium open; ornamentation costate, whole surface covered by minute granules. Test fibrous, impunctate.

Ventral interior.—Umbonal cavity shallow in young shells, deep in old; teeth moderately strong, wide, forming the margin of the delthyrial cavity; in many specimens the margins of the palintrope overhang the delthyrial cavity; crural fossettes shallow, oblique; dental plates strongly defined, with deep umbonal cavities in young shells, but in old ones they become obsolete by deposition of adventitious shell. Muscle marks rarely clearly defined; in young shells the muscle field is surrounded by a ridge extending from the anterior ends of the dental plates, and in old shells it is on a platform of adventitious shell. Adductor track broad, linear; diductor track elongate; adjustor marks not separable or on the sides of the delthyrial cavity. Pedicle callist visible in the apex; anterior margin and the whole interior of the shell costate in youth, but the costæ limited to the margins in old specimens. Interior of old shells marked by irregular ovarian pits or elongate pustules.

Dorsal interior.—Notothyrial cavity small, shallow; cardinalia small, confined to about the posterior one-fifth of the length of the shell; brachiophores grooved on the inside, not distinguishable from the supports which in young shells curve together to unite with the floor of the valve beneath the cardinal process as in *Plectorthis*; socket very shallow, defined by a small fulcral plate, umbonal cavities prominent in young shells; in old individuals all of the structures of the cardinalia are completely obliterated by adventitious shell. Cardinal process a simple low ridge, on each side of which are the diductor impressions, much resorbed in old shells. A low ridge divides the adductor scars medianly; in young shells this elevation corresponds to the median depression in the fold of the exterior, but in old shells it is a low fold of the inner shell layer, extending to a point a little forward of the middle; adductor scars unequal in size, the posterior pair the larger, divided from the anterior adductor impressions by low ridges at right angles to the median ridge. Ovarian impressions in the form of pits and elongate pustules.

GEOLOGIC RANGE.—Middle Ordovician (Black River) to at least Middle Silurian (Niagaran).

AMERICAN SPECIES

Unicostate group

- P. uniplicata* McEwan 1919
- uniplicata uticana* Ruedemann 1925

Bicostate group

Subgroup A

- P. precedens* McEwan 1919
- regularis* Shaler 1865
- daytonensis* Foerste 1885
- daytonensis laurelensis* McEwan 1919

Subgroup B

- P. trentonensis* McEwan 1919
- trentonensis perplana* McEwan 1919
- trentonensis champlainensis* McEwan 1919

Subgroup C

- Delthyris brachynota* Hall 1843
- Orthis biforata lynx* forma *reversata* Foerste 1885
- Platystrophia camerata* Twenhofel 1928

Subgroup D

- P. hermitagensis* McEwan 1919

Tricostate group

Low-fold subgroup

- P. minuta* Raymond 1921
- extensa* McEwan 1919
- globata* Twenhofel 1928
- elegantula* McEwan 1919
- elegantula triplicata* McEwan 1919
- elegantula amplisulcata* McEwan 1919
- amœna* McEwan 1919
- amœna longicardinalis* McEwan 1919
- globosa* McEwan 1919
- rhynchonelliformis* McEwan 1919
- colbiensis* Foerste 1910
- colbiensis mutata* Foerste 1910
- præcursor* Foerste 1910
- præcursor latiformis* McEwan 1919
- præcursor angustata* McEwan 1919

Maysville series

- P. juvenis* McEwan 1919
- pauciplicata* Cumings 1903
- strigosa* McEwan 1919
- nitida* McEwan 1919
- corryvillensis* McEwan 1919
- sublaticosta* McEwan 1919
- Orthis morrowensis* (James) 1874

Richmond series

- P. acuminata* (James) 1878
- foerstei* McEwan 1919
- foerstei ampla* McEwan 1919
- attenuata* McEwan 1919
- clarksvillensis* Foerste 1910
- cummingsi* McEwan 1919
- annieana* Foerste 1910
- lynx moritura* Cumings 1908
- acutilirata* (Conrad) 1842
- acutilirata prolongata* Foerste 1910
- senex* Cumings 1908
- elkhornensis* McEwan 1919

AMERICAN SPECIES—*Cont.*

Ponderosa subgroup

- P. preponderosa* McEwan 1919
ponderosa Foerste 1909
ponderosa auburnensis Foerste 1909
ponderosa arnhemensis McEwan 1919

High-fold subgroup

- P. profundosulcata* (Meek) 1873
profundosulcata hopensis Foerste 1910
crassa (James) 1874
laticosta (Meek) 1873
unicostata Cumings 1903
unicostata crassiformis McEwan 1919
cypha (James) 1874
cypha tumida McEwan 1919
cypha arcta McEwan 1919
cypha bellatula McEwan 1919
wallowayi Foerste 1912

EUROPEAN SPECIES

Unicostate group

- Porambonites costata* Pander
Spirifer chana Verneuil non Von Buch (Géol. Russie,
 pt. 2, pl. 5, fig. 1)

Tricostate group

- Terebratulites biforatus* Schlotheim
Platystrophia sublimis Öpik
P. biforata Reed (non Schlotheim) (Girvan Dist., p. 845)
Spirifer aperturata Schlotheim (Eichw. reports from
 Orthoceratites ls.)
Terebratula tenuicostata Eichwald
 ? *T. lynx* Eichwald
 ? *Platystrophia biforata sardoa* Vinassa de Regny

Bicostate group

- Porambonites dentata* Pander
Orthis biforata Davidson non Schlotheim (Brit. Foss.
 Brach. vol. 3, pt. 7, Sil., pl. 38, figs. 11a, b)
Spirifer tridens McCoy (may = *biforata*)
Spirifera biforata fissicostata McCoy¹⁵
Atrypa dorsata Hisinger¹⁶ (some of the forms placed
 here belong in *Oxoplectia*)
Platystrophia "biforata"—Silurian of Gotland

DISCUSSION.—*Platystrophia* is unique among the Orthidæ. At first referred to *Terebratulites*, *Terebratula*, *Spirifer*, *Delthyris*, etc., Davidson in 1848¹⁷ was the first to show that the internal characters of the shell were clearly orthoid. In 1850 King proposed the name *Platystrophia* for the group, basing it on *Terebratulites biforatus* Schlotheim. However, the proposal of the new generic term for this group was too radical a departure for the times. Hence one

¹⁵ *Orthis biforata* var. *fissicostata* Davidson non McCoy (Brit. Foss. Brach., vol. 3, pt. 7, Sil., pl. 38, figs. 15-17) may be an *Oxoplectia*.

¹⁶ *Platystrophia dorsata* Reed (Girvan Dist., pl. 8, fig. 25) non Hisinger is an *Oxoplectia*.

¹⁷ Bull. Soc. Géol. France (2), vol. 5, p. 323.

finds later on that these shells are referred to *Orthis* by Davidson. Eichwald, on the other hand, accepted the name and by the early eighties it was in general use.

The most unique external features of this genus are its spiriferoid form, best developed in *P. acutilirata*, and the nearly equal length of the interareas. There are, however, several species in which the hinge-line, instead of being wide and alate, is actually narrowed and the whole form of the shell is suggestive of *Orthorhynchula* and the rhynchonellids. Such a form is *P. globata* Twenhofel. It is by no means usual in the genus that the interareas are equal; the ventral palintrope is as a rule the longer. In some species the ventral interarea is curved and the dorsal beak is incurved exactly as in *Spirifer*.

The interior of *Platystrophia* links the genus intimately to *Plectorthis* and *Hebertella*, as best seen in young specimens (see pl. 12, figs. 16, 19). The ventral dental plates are discrete, continued directly to the floor of the valve and marked off by deep umbonal cavities. In the dorsal valve the brachiphores and their supporting plates are not divisible. The combined plates converge to form a sessile cruralium. The sockets are defined by a fulcral plate (see pl. 12, fig. 19). The only notable departure from the type of structure usual in *Plectorthis* is in the cardinal process. This is a low septum located on the middle of the notothyrial platform. It is so low that it could never have served as the seat of attachment of the diductor muscles. It is possible that this septum or process is a secondary development. Scars of diductor attachments on the notothyrial platform can be seen commonly in mature specimens. It is likely, too, that the impressions or grooves on the inside face of the brachiphores are in reality also impressions of the diductor muscles.

In old shells a riotous deposition of adventitious shell covers over all of the structures usually relied on in taxonomics. The umbonal cavities laterad to the dental plates and brachiphore supports are completely filled. This obliteration of essential characters by adventitious shell has caused the taxonomic relationships of *Platystrophia* to remain in obscurity for many years. Barring the fold and sulcus, a young *Platystrophia* and a mature *Plectorthis* are almost identical internally and externally. Young *Platystrophias* are strongly costate internally, exactly as in *Plectorthis*, but in old age all of this resemblance is lost. The microscopic structure of the shell is like that of the *Plectorthidæ* in being fibrous and impunctate. Mrs. McEwan states that "the inner surface is finely punctate"; nevertheless, thin slices of the shell prepared by the writers show no punctæ. McEwan probably refers to the megascopic pits which indent the inner surface of old shells, but these have no relation whatsoever to punctæ, and are a feature of many orthoid shells.

The genotype of *Platystrophia* selected by King is Schlotheim's *Terebratulites biforatus*, based on an en-

tire specimen apparently found in the drift and therefore without known locality and horizon. Verneuil, upon the advice of Von Buch, who saw Schlotheim's original specimen, states that it has five ribs in the sulcus. This is not a distinctive character, as many species share this peculiarity. Subsequent workers have found great difficulty in identifying their localized shells and in consequence have united different forms under the same name. Because of the lack of formation and locality of Schlotheim's type, McEwan suggested that a different species be selected as the genotype. She says (p. 388):

As it is impossible to determine what Schlotheim's type-specimen was it can not stand as the type of the genus. *Platystrophia laticosta* Meek is well known to all investigators of paleontology. As it possesses all the qualities necessary for a genotype, it is suggested that future workers regard it as such.

This suggestion brought a protest from Bather¹⁸ and a discussion of the genotype from Dietrich.¹⁹ The latter defines *P. biforata* (Schlotheim) as belonging to the low-fold sub-group of the tricostate division, having five costæ in the sulcus and six on the fold, and nine on the lateral slopes, as Von Buch had previously stated. Its locality is either the north German diluvium or the Baltic Ordovician. Dietrich's description follows:

Das in Berlin befindliche Original der *Platystrophia biforata* ist ein mässig erhaltenes Schalenexemplar von 22 mm. Breite, 16 mm. Höhe und 13.5 mm. Dicke. Es hat auf dem Sinus 5 gleichstarke ungespaltene Rippen, auf dem Wulst deren 6. Auf den Seitenflächen zählt man in beiden Klappen 9 scharfe Rippen. Um die glatten Wirbel herum verwischen sich alle Rippen; der Sinus ist dort seicht und am Delthyrium macht er einer kleinen Aufwölbung Platz, auf die die Rippen nicht hinaufgehen; diese erscheinen, soviel zu sehen ist, alle gleichzeitig und keine ist bevorzugt. Auf dem Wulst entwickeln sich die Rippen durch Teilung.²⁰

This redescription of the genotype and its suggested affinities with the tricostate, low-fold group of *Platystrophias* are the data that were needed to establish its position. Cumings, after considerable study of the American and European species, found that those from Europe usually differed from their American relatives in the costation pattern of the sulcus. On the basis of

this study he stated that the "presumptions are strongly in favor of its [the genotype of *Platystrophia*] being biplicate [bicostate]" (p. 18), and accordingly he restricted the term *biforata* to bicostate forms. If Dietrich's determination of the genotype as a tricostate form be correct, it is evident that the bicostate species of "*biforata*," will need to be replaced by new specific names.

Cumings' splendid monograph on the "Morphogenesis of *Platystrophia*" gave the first careful analysis of the genus. It was in this paper that the supposed marked difference between the American and European *Platystrophias* was first indicated. These ideas have been extended and elaborated by McEwan. According to Cumings, three divisions may be distinguished as follows: (1) uniplicate, (2) triplicate, and (3) biplicate. Since in the present work the term plication is restricted to a major undulation of the shell, such as a fold or the undulations of the shell in *Enteleutes*, we here suggest that these terms be altered to unicostate, tricostate, and bicostate. The three groups may then be defined as follows:

(1) *Unicostate group*.—Here there is one costa in the sulcus and two on the fold at the end of nepionic development, and this condition continues then throughout life.

(2) *Tricostate group*.—In this group the primary costa of the unicostate condition remains unmodified throughout life, but in the early neanic stage a costa is implanted on each slope of the sulcus. Simultaneously the two primary costæ of the fold bifurcate.

The tricostate group is merely a modification of the unicostate one but it is convenient to continue the two groups for their stratigraphic value. Under the tricostate group McEwan recognizes three subgroups: (a) low-fold, (b) high-fold, and (c) *Ponderosa*.

(3) *Bicostate group*.—Here the median costa of the sulcus of the early neanic shell bifurcates, and simultaneously a costa is implanted between the two primary costæ of the fold. Four subgroups are recognized by McEwan but a comprehensive study of the European forms would doubtless demonstrate the need for more subdivisions.

Cumings has shown that the nepionic shell of *Platystrophia* has the sulcus in the dorsal fold and a fold on the ventral. In the neanic stage, however, the costæ bounding the sulcus become elevated to form a fold, and with this change the median rib of the dorsal valve is depressed to form the lone costa of unicostate shells. From this fundamental unicostate type the tricostate and bicostate groups have evolved.

According to McEwan and Cumings, divergence of the tricostate and bicostate stocks must have taken place in early Ordovician or Upper Cambrian time, this because the modification of "the plications [costæ] of the fold and sinus [sulcus] takes place before the shell has reached a length of 1 mm." The tricostate group is thought to have diverged "from the ancestral

¹⁸ Geol. Mag., vol. 57, 1920, pp. 88-90.

¹⁹ Centralblatt f. Min., etc., 1922, pp. 123-124.

²⁰ (Translation) The original specimen of *Platystrophia biforata*, which is located in Berlin, is a fairly well preserved example about 22 mm. wide, 16 mm. long, and 13.5 mm. thick. In the sinus [sulcus] it has 5 equally strong, undivided ribs, on the fold there are 6. On the lateral slopes one counts 9 sharp ribs on both valves. About the beak all of the ribs disappear; the sulcus in that place is shallow and at the delthyrium it passes into a small swelling, on which the ribs do not go; so far as can be seen, these appear simultaneously and none is favored. On the fold the ribs develop by division.

stock much later than the biplicate [bicostate] group" as the uniplicate condition remains till the shell has reached a length of 1.2 to 1.5 mm. (p. 391).

Platystrophia first appears in the European Middle Ordovician (Kuckers formation, Brandschiefer) in well organized bicostate and tricostate species, *P. dentata* and *P. lynx*. In the Schuchert Collection is a lot of *P. dentata* labelled as "probably Echinosphærites limestone." If this horizon be correct, it pushes the first appearance down into lower Middle Ordovician or about the time of the Black River in America. These Echinosphærites limestone specimens are bicostate forms and would not afford notable support to McEwan's theory concerning the origin of the group. The Kuckers may be upper Black River in age but is more probably lower Trenton. According to McEwan (p. 400), "a uniplicate species was found to occur in the Jewe [Trenton], and one specimen was found which occurred in the Upper Ordovician (F¹) [Lyckholm or uppermost Trenton]." The unicastate group therefore appears to be a rather insignificant assemblage. Both Cumings and McEwan maintain that the bicostate group is the dominant one in Europe. The foreign species are so poorly known that it is as yet difficult to know what is the dominant group in the way of species, but it is a fact that after their origin the bicostate group held the European ground occupied from the Middle Ordovician into the Middle Silurian. In North America, however, the situation is just the reverse, the tricastate group holding its ground throughout the Middle Ordovician and into the Middle Silurian.

McEwan's table (pp. 402-404) indicates the first appearance of *Platystrophia* in North America in Black River time (Decorah shale of Wisconsin). Hall and Clarke,²¹ Winchell and Schuchert,²² Ruedemann,²³ and Schuchert²⁴ all have reported *Platystrophias* from the Chazy but neither McEwan nor Cumings²⁵ could find any evidence to substantiate these reports. There may also be some doubt as to the precise age of the form *P. extensa* McEwan, said to have come from the Decorah shale. This formation has recently been subjected to a critical survey by G. Marshall Kay,²⁶ who comes to the conclusion that the upper or Ion member of the Decorah is actually lower Trenton in age. Kay reports *P. extensa* McEwan from this member (upper Ion, Prasopora faunule, Church, Iowa) in company with *P. trentonensis* McEwan. This is the only horizon from which he has *Platystrophia* and it is therefore probable that the specimen from the Decorah of Wisconsin is from the Ion member and actually lower

Trenton in age. This would be in agreement with the remarks made above on the European section.

In North America the first *Platystrophias* to appear, barring the one mentioned above, are bicostate forms in the lower Trenton and one unicastate species, *P. uniplicata* McEwan. If the so called Black River form be considered lower Trenton in age, then the three groups appear in North America almost simultaneously and fully standardized. The unicastate group is represented here by one known species only. After lower Trenton time the bicostate group is, so far, unknown in the American Ordovician until the topmost formation, the Gamachian (Ellis Bay) of Anticosti, is reached. From this time on the bicostate group is dominant in American Silurian strata and a very few rare tricastate individuals are to be found in the early Silurian.

A recent table of suggested correlations by Ulrich²⁷ places the Wierland group, of which the Echinosphærites limestone and Kuckers are a part, as upper Chazy in age. This would make the European species antedate the American forms and would be rather suggestive, although not final evidence, of a European origin of the genus. The important point, however, is not the precise age of their appearance but the fact that, when *Platystrophias* are present for the first time, the three groups come together, fully organized.

The appearance of *Platystrophia* in early Trenton, Black River, or late Chazy time is suggestive that the ancestor of the group should be sought in rocks of Chazy age. McEwan has prophesied a unicastate progenitor, from which the bicostate group diverged first, followed by the tricastate group.

Both Cumings and McEwan have turned to the Upper Cambrian faunas as being the possible source of *Platystrophia*. Cumings found in *Orusia lenticularis* (Wahlenberg) "a form that possesses in the adult practically all of the nepionic characters of *Platystrophia*" (p. 5). Taking only external characters, this form could have evolved the exterior of *Platystrophia*, and internally it has subparallel, discrete brachiophore plates, not unlike those of *Platystrophia*. It is possible, of course, that crowding of the bases of these toward each other could produce the condition seen in *Platystrophia*, but the early appearance of *Orusia* and its short stratigraphic range make it unlikely that it is the direct ancestor, although it may have been in the general line.

Cumings has also pointed out the external similarities between *Platystrophia* and *Plectorthis*, as follows (pp. 11-12):

In some respects the adult *Plectorthis plicatella* resembles the neanic *Platystrophia*. If the fold and sinus be disregarded (and in some Trenton forms of *Platystrophia* these are surprisingly inconspicuous), the neanic *Platystrophia* is almost a *Plectorthis*. There is little doubt that

²¹ Pal. N. Y., vol. 8, pt. 1, 1892, p. 202.

²² Geol. Minn., vol. 3, pt. 1, 1895, p. 456.

²³ N. Y. State Mus., Bull. 49, 1902, p. 25.

²⁴ U. S. Geol. Surv., Bull. 87, 1897, p. 309.

²⁵ Amer. Jour. Sci. (4), vol. 15, 1903, p. 5.

²⁶ Jour. Geol., vol. 37, 1929, pp. 639-671.

²⁷ U. S. Nat. Mus., Proc., vol. 76, 1930, p. 73.

when the nepionic shell of *Plectorthis* is discovered it will be found to be quite indistinguishable from the nepionic shell of *Platystrophia*, since the two groups present at the beaks almost identical characters. . . *Plectorthis* may therefore represent an offshoot from the *Platystrophia* group near its initiation or, . . . it may have been separately derived from the *Orthis* [*Orusia*] *lenticularis* stock.

The writers of the present work have gone even farther than Cumings and show that the internal characteristics of *Plectorthis* and *Platystrophia* are almost identical. These facts link the two genera intimately, but it is impossible at present to say if the one was derived from the other. We are suggesting the origin of the Plectorthidae in general from the Ozarkian *Finkelnburgia*, which has all the internal characteristics of *Plectorthis* and *Platystrophia*.

Wysogorsky²⁸ looked to *Orthis calligramma* as the ancestor of *Platystrophia*, but his view is not tenable since that species does not have internal characters from which those of the genus under consideration could be derived. The development of a strong fold and sulcus is not the whole story in the evolution of this genus. McEwan states (p. 388) that "*Eoorthis* of the Upper Cambrian has the physiognomy of this genus and has been confused with it." It must be emphasized, however, that the Orthidae and Billingsellidae with their peculiar type of divergent brachiophores could never have evolved *Platystrophia*.

Öpik²⁹ gives the origin of *Platystrophia* from "*Orthis*" *recta* (Pander) as follows:

Der Ursprung von *Platystrophia* ist in der Gruppe der "*Orthis*" *recta* (Pander) aus B_{1β} and B_{11a} des Ostbaltikums zu suchen. Unwahrscheinlicher ist die Ableitung aus *O. calligramma* oder *Orusia*.³⁰

"*Orthis*" *recta* is the type of our new genus *Angusticardinia* (1931). Internally it has features that might lead to plectorthoid structures. The brachiophore supports are convergent but meet a short median ridge. The specimens at hand are too poorly preserved to show socket plates but such may have existed. Externally, however, *Angusticardinia* has none of the requisite features for the *Platystrophia* ancestor. There is a more or less well defined sulcus on each valve, the one of the dorsal having as many as three costæ. It seems to be rather a plastic form, diverging toward the rhynchonellids. Its only truly orthoid features are the two interareas with their open delthyria. Internally the dorsal valve is not unlike the early rhynchonellid species *Camarotoxechia* ? *plena* (Hall) and *C. ? orientalis* (Billings). Accordingly we hold that

Angusticardinia is not the ancestor of *Platystrophia* but probably a divergent stock of the Orthidae toward the rhynchonellids.

It is therefore impossible as yet to indicate the place of origin for *Platystrophia*, but it seems more probable that it was western Europe than northeastern North America. On the other hand, there may have been two origins, the American forms arising out of the stock that gave rise to *Plectorthis* and the European forms independently out of some unknown stock.

Genus MCEWANELLA Foerste 1920

Pl. 12, figs. 11, 12, 17, 18, 21, 22

Foerste, Bull. Sci. Lab. Denison Univ., vol. 19, 1920, p. 197.

GENOELECTOTYPE (Schuchert and LeVene 1929). —*Platystrophia fernvaleensis* McEwan 1919, Proc. U. S. Nat. Mus., vol. 56, p. 428, pl. 50, figs. 1-3 = *Hebertella lineolata* Savage 1918, Trans. Illinois Acad. Sci., vol. 10, p. 267, pl. 1, figs. 1, 2.

DESCRIPTION. *Exterior*.—*Platystrophiinae* with the whole surface multicostellate, the costellæ covering the inherited *Platystrophia* costæ or constituting all of the ornamentation.

Interior.—The ventral musculature and dorsal cardinalia are exactly like those of *Platystrophia*, but in mature shells there appears to be very little deposition of adventitious shell.

GEOLOGIC RANGE. — Upper Ordovician (Richmond).

AMERICAN SPECIES

Hebertella lineolata Savage 1918 (syn. *M. fernvaleensis* McEwan 1919)

McEwanella raymondi Foerste 1920

DISCUSSION.—*McEwanella* was separated from *Platystrophia* chiefly because of its peculiar ornamentation. At the beaks the shell is usually costate as in *Platystrophia*, but in all later growth the costæ are completely altered by bifurcation into costellæ. In some specimens of *M. lineolata* the primary costæ may be lost at the front of the shell and the whole surface is then occupied by costellæ. This is a radical departure from the costate and granulose surface of *Platystrophia*. The surface of *McEwanella* is a convergence toward the type of ornamentation usual in *Eoorthis*, and so well shown by *E. ochus* Walcott from the Ozarkian. In *M. raymondi* the primary plications are strongly developed over the whole surface of the shell.

Internally, *McEwanella* is clearly a *Platystrophia*. The ventral muscle field has a similar thickened ridge and the individual impressions have the same indistinctness. The cardinalia have rather sharply pointed, elongate brachiophores which have the supporting

²⁸ Zeit. deut. geol. Gesell., vol. 52, 1900, p. 234.

²⁹ Acta et Comment. Univ. Tartuensis, A, vol. 17, pt. 1, 1930, p. 102.

³⁰ (Translation) The origin of *Platystrophia* is to be sought in the group of "*Orthis*" *recta* (Pander) from B_{1β} and B_{11a} of the east Baltic region. Less probable is the derivation out of *O. calligramma* or *Orusia*.

plates convergent and uniting under the cardinal process. The latter is a thick ridge with an unexpanded myophore as in *Plectorthis*. The sockets are defined by fulcral plates.

One interesting variation between mature *Platystrophia* and *Mcewanella* is found in the different degree in which the two genera thicken the shell. In nearly all *Platystrophias*, even the small Russian species, this thickening may go on to a prodigious degree. But in the largest dorsal valve of *Mcewanella* studied, which is 35 mm. wide, there is practically no deposition of adventitious shell, the delicate little fulcral plate being readily visible. This variation of growth habit emphasizes the generic distinction between the two groups.

It is obvious from the decided similarity in both the internal and external characters of *Mcewanella* and *Platystrophia* that the origin of the former should be sought in one of the groups of *Platystrophia*. According to McEwan's view (p. 429) "the greater strength of the median plications suggests that it [*M. lineolata*] belongs to the Triplicate Type." In her table on p. 403 she places *M. lineolata* (her *P. fernvalensis*) in the Ponderosa subgroup of the tricostate division. We have studied McEwan's material and are of the opinion that this species belongs in the unicostate division. A ventral valve (a specimen figured on pl. 50, fig. 1) has a prominent median rib in the sulcus. A dorsal valve (pl. 50, fig. 3) shows two costæ on the fold at the rear third of the shell but these are broken into costellæ at the front which occupy the whole sulcus.

The other species, *M. raymondi*, indicates the group affinities much more closely than *M. lineolata*. Here the dorsal valve as figured by Foerste³¹ has two costæ in the fold, while a ventral valve collected by Ulrich from the top of the Kimmswick at Cape Girardeau, Missouri (pl. 12, fig. 17), has a prominent median costa in the sulcus. It would appear therefore that *Mcewanella* came out of the unicostate division rather than the tricostate one.

The Kimmswick limestone, from which *M. raymondi* is said to have come, is usually regarded as of Trenton age, and if so, *Mcewanella* arose near the time of origin of the *Platystrophias*. On the other hand, the upper Kimmswick (the horizon carrying *Mcewanella*) may be of Richmond age. In any event, the two species of *Mcewanella* are of one genetic line, showing origin in the unicostate group of *Platystrophia*.

Subfamily ORTHOSTROPHIINÆ Schuchert and Cooper 1931

Convexo-concave to unequally biconvex Plectorthis, having confined ventral musculature and dorsal muscles elevated on a callosity. Both valves have

complicated pallial markings, which resemble those of *Mimella* in the ventral valve, and it is on the basis of this feature that *Orthostrophia*, the only genus of this subfamily, is placed in association with the members of the Plectorthisidæ.

GEOLOGIC RANGE.—Silurian into Lower Devonian.

Genus ORTHOSTROPHIA Hall 1883

Pl. 6, figs. 22-25, 27, 28, 31; t. fig. 7

Hall, 2d Ann. Rept. N. Y. State Geol., 1883, pl. 36, figs. 32-34.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, p. 199, pl. 5A, figs. 24-27, pl. 6, figs. 32-34.

GENOHOLOTYPE.—*Orthis strophomenoides* Hall 1857, 10th Rept. N. Y. State Cab., p. 46.

DESCRIPTION. *Exterior*.—Shell sub-strophomenoid, hinge-line straight and wide, cardinal extremities rounded or obtuse, slightly deflected; lateral profile convexo-concave or subequally biconvex; anterior commissure uniplicate or sulcate; fold and sulcus frequently the reverse of the normal. Beaks incurved, commonly approximate. Ventral area the longer, apsacline; dorsal area shorter, orthocline or apsacline; delthyria and notothyria open; ornamentation multicostellate; costellæ and interspaces crossed by elevated concentric lines of growth.

Ventral interior.—Delthyrial cavity shallow or deep; teeth strong, dental plates thick, obscured by adventitious deposit; umbonal cavities almost completely obliterated in old shells; muscle area confined, adductor track linear, expanding in front; diductor tracks small, subtriangular; pallial markings prominent, two main trunks extending forward from the ends of the diductors and two other trunks extending anteriorly but soon bifurcating, each of the branches sending out ramifications. Between the two lateral trunks are two minor sinuses.

Dorsal interior.—Notothyrial cavity shallow, cardinalia thickened, brachioophores thick, blunt, sockets shallow; cardinal process linear, expanded anteriorly; there is not uncommonly a small ridge on either side of the cardinal process, as in *Schizoramma*. Muscle area confined, deeply impressed, the margins of the field being thickened and elevated. Adductor scars subequal in size, the anterior pair usually the more clearly impressed and the more elongate. Pallial markings strongly impressed; two large divergent trunks extending anteriorly from the antero-lateral ends of the anterior adductors, and each sending off three or four branches which bifurcate near the margin, each bifurcation in turn sending off ramifying branches. On each side of and adjacent to the muscle area in the umbo-lateral spaces is a more or less circular ovarian area marked by raised dendritic lines.

GEOLOGIC RANGE.—Silurian into Lower Ordovician of eastern North America.

³¹ Bull. Denison Univ., vol. 19, 1920, p. 198, pl. 23, fig. 1.

SPECIES

Orthostrophia canadensis Clarke 1907

O. dartæ, n. sp.

O. dixonii Foerste 1909

O. netesomensis Foerste 1909

O. strophomenoides (Hall) 1857

DISTINGUISHING CHARACTERS.—The characteristic features of *Orthostrophia* are the unequally biconvex or convexo-concave profile, the small, deeply impressed muscle field in the ventral valve, and the muscular area of the dorsal valve which is elevated on a deposit of adventitious shell. More fundamental than all of these, however, are the pallial and ovarian impressions described in detail below.

DISCUSSION.—The simple ventral musculature and the cardinalia in *Orthostrophia* seem to relate this genus most closely to *Orthis*, *Hesperorthis*, and their allies. Confined to a short and deeply impressed delthyrial cavity, the individual muscle-scars are not strongly impressed on the shell and in some specimens they can not be individualized. When the separate scars are visible, only two sets can be seen. The median or adductor track is triangular, rounded and wide in front. The "diductors" are narrow and sub-crescentic. It is possible that the wide central track is the equivalent of the combined adductors and diductors and that the scars usually referred to as diductors are actually adjustor scars; we are not able to prove this at present.

The cardinalia appear to be orthoid. The brachio-phores are simple processes supported by adventitious shell, and the sockets are between the sloping outer face of the brachio-phore and the shell wall. The cardinal process is a simple linear ridge, but in some shells may be supplemented by oblique accessory elevations such as are seen commonly in *Schizorammina*.

The dorsal musculature of *Orthostrophia* is decidedly orthoid in character but has the usual feature of bipartite anterior adductors, discussed at length under *Productorthis* and *Schizophoria*.

The pallial markings have considerable resemblance to those of *Dinorthis* (*Plæsiomys*) and *Mimella*. Their detail is described on an earlier page. The combination of characters in *Orthostrophia* relate it to the Orthidæ and Plectorthidæ, and it is placed tentatively in the latter family, mainly on the basis of the pallial marks.

Orthostrophia dartæ, n. sp.

Pl. 6, figs. 23, 31

Shell small, thin, biconvex, subelliptical to subcircular in outline. Ventral valve with a well defined fold in the young stages which develops into a sulcus at the front. In the dorsal valve there is a sulcus at the beak and for half the length of the valve, which then develops into a prominent fold produced beyond

the anterior margin. Surface multicostellate, six or seven costellæ in 5 mm. at the front of the shell. Ventral muscle field confined, about one-fifth the total length of the shell. Adductor scars small.

Measurements:

| | Length | Width |
|----------|--------|--------|
| Holotype | 19 mm. | 21 mm. |
| Paratype | 15 | 20 |

This form occurs in the Middle Silurian of Port Daniel, Gaspé Peninsula, Quebec. It is named for Miss J. Doris Dart, who assisted Professor Schuchert in making known the Silurian stratigraphy of the scenic Port Daniel area.

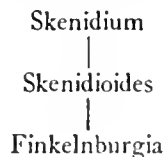
Family SKENIDIIDÆ Kozłowski 1929

Small subpyramidal Orthacea probably derived out of *Finkelburgia*, having a spondylium, a cruralium, and fulcral plates forming the sockets.

GEOLOGIC RANGE.—Middle Ordovician into Lower Devonian.

This small family embraces the genera *Skenidioides* Schuchert and Cooper and *Skenidium* Hall. At first sight they appear to be tiny clitambonitoid shells and best referred to the Clitambonacea, but the interior characters of the dorsal valve appear to indicate that they are more closely related to the Plectorthidæ or even the older genus *Finkelburgia*, hence we accept the place given them by Kozłowski.

The evolution of the family appears to be as follows:



Genus SKENIDIoidES Schuchert and Cooper
1931

Pl. 10, figs. 6, 8, 10-14

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 243.

GENOHOLOTYPE.—*S. billingsi* Schuchert and Cooper 1931.

DESCRIPTION. *Exterior.*—Small, semi-elliptical, hinge-line straight. Cardinal extremities acute or nearly a right angle. Lateral profile unequally biconvex, plano-convex, or slightly concavo-convex. Anterior commissure sulcate; ventral fold gentle, rounded, sulcus deep or shallow. Ventral palintrope strongly apsacline or catacline; beak may or may not be incurved; delthyrium open. Dorsal palintrope short, anacline, notothyrium open. Surface multicostellate; test fibrous, impunctate.

Ventral interior.—Teeth strong, located at the angle formed by the delthyrial and hinge margins. Dental lamellæ forming a shallow spondylium simplex, supported at the rear of the shell but free at the front. Muscle-scars borne on the spondylium.

Dorsal interior.—Notothyrial cavity shallow, brachiophores long and slender, supporting plates converging and uniting with the median septum to form a cruralium. Cardinal process linear, prolonged toward the front as a prominent median ridge; myophore a compressed crenulated area. Sockets defined by a concave socket plate.

GEOLOGIC RANGE.—Middle Ordovician (Stones River) to Silurian (Niagaran: Wenlock and Lockport).

AMERICAN SPECIES

Skenidioides billingsi Schuchert and Cooper 1931

Skenidium anthonense Sardeson 1892

S. halli Safford 1869

S. pyramidalis (Hall) 1852

?? *O. merope* Billings (may be a *Hesperorthis*)

EUROPEAN SPECIES

Skenidium craigensis Reed 1917

S. greenoughi Reed 1917

Orthis lewisii Davidson 1848

DISTINGUISHING CHARACTERS.—This group of tiny shells has been usually identified with *Skenidium* and externally its members do form a rather precise homœomorph with those of that genus. Internally, however, *Skenidioides* differs from *Skenidium* in not possessing the marked hinge-plate so characteristic of the latter. Along with the decided development of the hinge-plate in *Skenidium* has gone the loss of the dorsal interarea, which is, however, well developed in *Skenidioides*.

DISCUSSION.—It is important to bring out in greater detail here several points about the shell of *Skenidioides*, leaving the detailed comparison of the two genera to the discussion under *Skenidium*. The spondylium of *Skenidioides* is rather shallow and hangs freely into the body chamber at its front end; at the posterior end it is supported either by an abbreviated stout septum, or by adventitious shell, forming a callosity beneath the plate. The spondylium is attached to the ventral surface of the palintrope along the outside of the ridge formed by the progressive growth of the teeth. The edges of the delthyrium are the inner margins of the tooth ridges which project into the delthyrial cavity when the whole structure is viewed from the front or in section.

In the dorsal valve the cardinalia are distinctive. The brachiophore supports are discrete plates meeting a high median septum. At the posterior of the valve the cruralium rests on the inner surface of the valve or on a callosity of adventitious shell deposited in the

cavity between the plates and valve. The fulcral plates are like those in *Plectorthis* and the socket may be covered over by the margin of the palintrope. The median ridge and cardinal process form a continuous partition which effectively divides the shell into a right and left half. The adductor scars, according to Kozłowski's figure of *Skenidium lewisii*,³² are located on each side of the median septum. The anterior scars are located postero-laterally of the other pair.

The brachiophores and supporting plates are like those of *Plectorthis* and lead to the inference that *Skenidioides* is a branch from the early *Plectorthis* stock, or better, from the earlier *Finkelburgia*, as Kozłowski suggests. *Skenidioides* developed along the line of perfecting the spondylium and cruralium, but is, nevertheless, wholly unrelated to any of the Clitambonitidæ or Pentameracea where it was previously classified. Placement near the Plectorthidæ is justified because of the complete lack of a deltidium or chilidium and the plectorthoid character of the cardinalia. It has been shown under the Clitambonitidæ that the brachiophores characteristic of this family are orthoid and that their support is accomplished, not by plates, but by adventitious shell which swells laterally from the notothyrial platform. In *Skenidioides* the brachiophore plates form a decided cruralium, and in *Skenidium* there is a distinct hinge-plate, both features being foreign to the Clitambonitidæ but clearly derivable from the Finkelburgiæ or Plectorthidæ.

Skenidioides billingsi Schuchert and Cooper 1931

Pl. 10, figs. 6, 8, 10-14

Shell rather small, semicircular in outline, biconvex in lateral profile. Ventral interarea long and broad, strongly apsacline; delthyrium open. Dorsal valve less convex than the ventral, with a rather short interarea. Surface marked by about 28 low costellæ, a few of which bifurcate beyond the middle of the shell. The ventral valve is provided with a low median elevation and the dorsal valve is rather deeply sulcate.

This shell is distinguished from *S. anthonense* (Sardeson) by its larger size, coarser ornamentation, and less proportionate width to its length.

Measurements:

| | Length | Width | Thickness |
|----------|---------|-------|-----------|
| Holotype | 5.5 mm. | 8 mm. | 3.5 mm. |
| Paratype | 4.5 | 7.5 | |

S. billingsi comes from rocks of Black River age, at Paquette Rapids, Ottawa River, Quebec. The holotype is Cat. No. 2013a, Schuchert Collection, Yale University.

³² Pal. Polonica, vol. 1, 1929, p. 48.

Genus SKENIDIUM Hall 1860

Pl. 13, figs. 1-5, 8

Hall, 13th Rept. N. Y. State Cab., 1860, p. 70, figs. 2, 4, 5 (not 1, ?3).

Kozłowski, Pal. Polonica, vol. 1, 1929, pp. 46-51.

GENOLECTOTYPE (Hall and Clarke).—*Orthis insignis* Hall 1859, Pal. N. Y., vol. 3, p. 173.

DESCRIPTION. *Exterior*.—Shell small, subpyramidal, semicircular or semielliptical in outline; hinge-line straight; cardinal extremities usually acutely angular, not uncommonly subauriculate. Lateral profile subtriangular; ventral valve triangular, gently convex; dorsal valve gently convex or plane. Anterior commissure sulcate. Ventral palintrope long, strongly apsacline to procline; dorsal palintrope nearly obsolete. Surface ornamentation consisting of simple or dichotomous costæ; test fibrous, impunctate.

Ventral interior.—Like *Skenidioides* in possessing a spondylium completely free at the front but supported at the rear by an abbreviated septum.

Dorsal interior.—Notothyrial cavity small and shallow; brachiophores long and slender, supporting plates shallow, meeting the median septum. Cardinal process a linear ridge not continuous with the median ridge. Outside the brachiophores are concave plates; between these and the wall of the valve is located the socket which is formed by a fulcral plate. Adductor scars were not observed.

GEOLOGIC RANGE.—Lower Devonian of eastern North America and ? Russia.

AMERICAN SPECIES

Skenidium insigne (Hall) 1859

FOREIGN SPECIES

? *S. uralicum* Tschernyschew 1887

DISTINGUISHING CHARACTERS.—*Skenidioides* was separated from *Skenidium* chiefly because it does not possess the peculiar hinge-plate characteristic of the dorsal valve of the latter. There are also minor differences in the ventral valve. For example, in *Skenidium* the spondylium at the posterior extremity of the valve fills the delthyrium and is flush with the surface of the palintrope. In *Skenidioides*, on the other hand, this plate is always depressed below the level of the interarea. The spondylium of *Skenidium* in its growth forward, however, becomes depressed below the interarea and its free end is attached to the outside of the ridges formed during the progressive growth of the teeth.

In the dorsal valve the development of a flat or flatly concave plate between the outside margins of the brachiophores and the walls of the valve produces the prominent hinge-plate characteristic of the genus. The brachiophore supports are shallow and their inner mar-

gins are upturned where they unite with the median ridge. The cardinal process appears to be formed of their united upturned edges. The cardinal process and median septum are not therefore continuous. The median septum divides the valve into two halves as in *Skenidioides*.

DISCUSSION.—Hall and Clarke maintained that *Skenidium* evolved from *Orthis merope* Billings through *S. halli* (Safford) to *S. pyramidalis* (Hall). This genetic evolution, however, is not so simple, since *Orthis merope* is preceded in time by *S. halli* from the Stones River (Glade limestone) of Tennessee and *S. anthouense* (Sardeson) from the Black River of Minnesota. To the more primitive forms such as *S. halli* and *S. anthouense* the writers have given the name *Skenidioides*. It is likely that *Skenidium* developed directly from *Skenidioides*. The *Orthis merope*, on the other hand, appears to belong to a stock related to *Hesperorthis* rather than to *Skenidium*.

Skenidium and *Mystrophora* have usually been treated as synonyms, but the endopunctate shell and lobate cardinal process of the latter indicate that it is a development parallel to *Skenidium* out of some dalmanelloid stock. *Mystrophora* is accordingly placed in the Dalmanellacea.

**Family ORTHIDÆ Woodward 1852,
emended**

(Orthinæ (partim) Waagen 1884)

Progressive and terminal Orthacea derived probably out of the Eoorthinæ, with interareas on both valves; nearly all have open delthyria, oval or obcordate ventral muscle fields, subreniform ovarian impressions, and subparallel median pallial sinuses. In the dorsal valve the cardinal process is a simple linear ridge directed ventrally; the brachiophores are rodlike, divergent, and without support other than the adventitious shell substance of the notothyrial platform; chilidia are of rare occurrence.

The family may have had its origin in the Middle and certainly in the Upper Cambrian and appears to have died out with the Silurian.

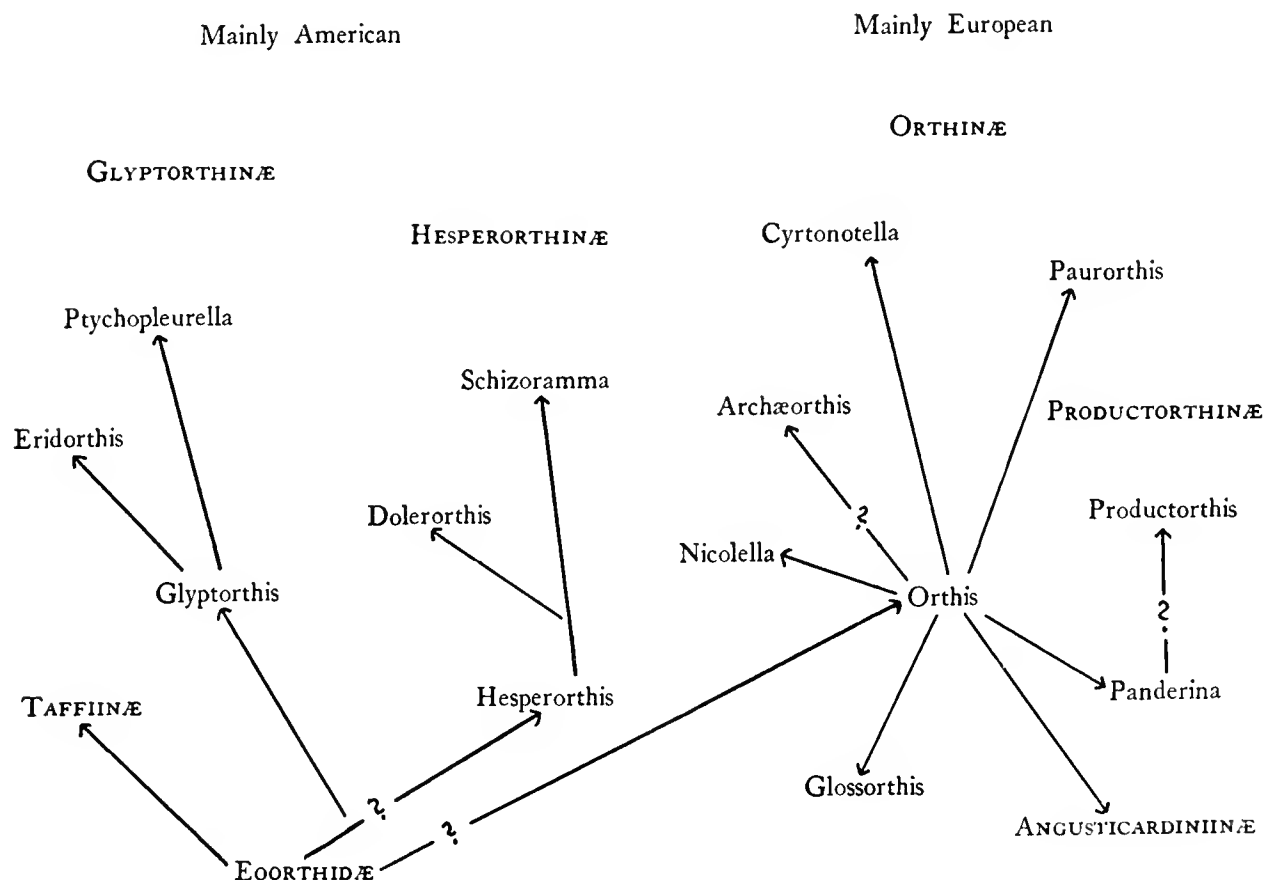
The family Orthidæ as here emended is rather radically reorganized and greatly restricted. Some of its previously familiar members such as *Plectorthis*, *Hebertella*, and *Platystrophia* have been placed in the new family Plectorthidæ. Such changes as these have been brought about by a closer analysis of the internal structures of the shell than any hitherto made, and a more precise definition of the cardinalia.

We base family characters on the gross internal morphology, and to differentiate the genera we use the highly variable external form, plus smaller details of the interior.

Perhaps the most striking variation within the Orthidæ is that of *Productorthis*, which externally simulates the contour, profile, and sculpture of certain genera in the Productidæ but never bears the prominent tubular spines of the latter.

terior and lateral margins of the ovarian impressions. The subparallel pallial sinuses are homologous with the widely divergent marks of the Billingsellidæ, and originate at the front of the diductor scars as in that family. The septum separating the two sinuses may

Table 5



In the ventral valve the muscle-scars are usually confined to the delthyrial cavity. The diductor impressions may or may not be prolonged in front of the adductor track, but they never swing around in front to enclose the diductors as in the Dinorthidæ. Adjustor scars are usually not clearly defined but are fairly definite in some of the younger genera. Occupying the umbo-lateral spaces and produced nearly to the front and lateral margins are subreniform ovarian impressions. These are bounded on the inside and antero-median margins by prominent pallial sinuses. The latter take their origin at the front ends of the diductor tracks, as is usual in orthoid brachiopods, extend forward nearly parallel, and are separated by a very narrow ridge or low septum only. At the front of the valve each sinus swings abruptly laterally and extends for a longer or shorter distance along the an-

be broad or wide and is forked at the front or not, depending on the age of the shell or how deeply impressed the sinuses are at that point.

In the dorsal valve the brachiophores are usually simple, rodlike, or narrow and bladelike; they are closely related to those of the Billingsellidæ but appear to be more highly specialized. Support of the brachiophores is accomplished by deposition of adventitious shell substance under their antero-dorsal surface and upon the notothyrial platform. The cardinal process is always a simple septum which may or may not bear the diductor scars; impressions of these are frequently to be seen on the notothyrial platform on either side of the cardinal process at its base. Dorsal pallial impressions are too infrequently seen to serve importantly in any family definition.

Derivation out of the Billingsellidæ is demonstrable

by homologizing the muscle impressions and pallial sinuses of the ventral valve and the cardinalia. Remnants of deltidia within the Orthidæ are further links of relationship with the Billingsellidæ. The cardinalia of *Billingsella* and *Eoorthis* are enough like those of the Orthidæ to hold that the one could have been derived out of the other. We believe it probable that the Hesperorthinæ and Glyptorthinæ were derived from *Eoorthis* of the Eoorthidæ, but the Orthinæ of Europe appear to us to have been derived out of *Billingsella* or some unknown ancestor closely related to that genus. The origin of the Orthidæ can not be stated with any degree of precision because the Cambrian and Ozarkian articulate brachiopods and Cambrian and Ozarkian stratigraphy of the world are too little known at present to warrant more than suggestions.

We propose to subdivide the family Orthidæ into the following subfamilies, all of Schuchert and Cooper 1931:

| | |
|------------------|---------------|
| Orthinæ | Taffinæ |
| Productorthinæ | Hesperorthinæ |
| Angusticardininæ | Glyptorthinæ |

The lines of genetic descent seem to be about as shown in Table 5.

Subfamily ORTHINÆ Schuchert and Cooper 1931
(Not Orthinæ Waagen 1884 = mainly Orthidæ)

Progressive Orthidæ having short and strongly curved ventral interareas, with strongly incurved ventral beak. So far as known, a deltidium or any remnant of such a structure has never been seen in the Orthinæ as here defined. Chilidial plates are also rare in occurrence.

GEOLOGIC RANGE.—Lower and Middle Ordovician.

The members of the Orthinæ are chiefly European in origin and differ quite markedly in the contour and profile of the shell from the representative American stock typified by *Hesperorthis*. The European genera invariably have short curved interareas and are never provided with a deltidium or complete chilidium.

The subfamily contains the following genera:

Orthis Dalman
Cyrtotonotella Schuchert and Cooper
Nicolella Reed
Glossorthis Öpik
Paurorthis Schuchert and Cooper
? *Archæorthis* Schuchert and Cooper

Genus ORTHIS Dalman 1828 (sensu stricto)

Pl. 2, figs. 7-13, 15-18; t. figs. 3, 11

Dalman, K. Vet. Akad. Handl. for 1827, 1828, pp. 93, 96, pl. 2, fig. 3.

Davidson, Brit. Foss. Brach., vol. 1, Introd., 1853, p. 101, pl. 7, fig. 127.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, pp. 191-194.

GENOLECTOTYPE (Davidson). — *Orthis callactis* Dalman as above cited.

DESCRIPTION. *Exterior*.—Subsemicircular to semi-oval, anterior margin convex; lateral margins convex to concave; hinge-line wide and straight, rarely subulate; lateral profile plano-convex to unequally biconvex, occasionally concavo-convex; lateral commissure usually straight; anterior commissure rectimarginate, dorsal valve provided with a faint median sulcus. Ventral interarea short but longer than the dorsal one, curved; ventral umbo swollen, beak strongly curved, interarea faintly apsacline or nearly orthocline; delthyrium open. Dorsal interarea plane, strongly anacline, notothyrium open. Ornamentation paucicostate, costæ and interspaces covered by parvicostellæ and faint lines of growth. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep, teeth strong, crural fossettes very deep; dental plates strong, obsolete in old shells; muscle area confined to the delthyrial cavity, oval in outline; adductor scars centrally situated, forming an elongate track; diductor impressions extending as far forward as the end of the adductor track, and partially placed on the sides of the dental plates; adjustor scars not distinguishable; pedicle callist rarely visible in the apex. Pallial markings consisting of two trunks, one given off from the front end of each diductor scar and extending beyond the middle of the shell, where they are abruptly curved away from each other. Anterior margin crenulated by coarse ribs corresponding to the striæ of the exterior, each rib bearing an elevated ridge on its margin.

Dorsal interior.—Notothyrial cavity shallow; cardinalia confined; sockets deep, excavated slightly beneath the palintrope; brachiophores forming the margin of the notothyrial cavity, short and simple, unsupported except for the deposition of shell material around them in the building up of the notothyrial platform; cardinal process a simple ridge of variable thickness, probably bearing two muscle attachments; in some species diductor scars are visible on the notothyrial platform on each side and at the base of the cardinal process. Notothyrial platform a thickening of the valve forming the floor of the notothyrium, extended forward to the anterior margin of the adductor scars as a median ridge. Muscle area small, not occupying more than one-third the length of the valve; adductors small, the anterior pair the larger. Pallial markings four, one pair given off from the antero-lateral margin of the anterior adductors, the other from the anterior end of the median ridge.

GEOLOGIC RANGE.—Lower and Middle Ordovician.

AMERICAN SPECIES

O. buttsi, new name³³

O. panderiana Hall and Clarke 1892

³³ For *O. crasicosta* Butts (non Pander), Geol. Surv. Alabama, Spec. Rept. 14, 1926, p. 116, pl. 26, figs. 14-15.

EUROPEAN SPECIES

O. æqualis Pander 1830
O. callactis Dalman 1828
O. calligramma Dalman 1828
O. eminens Pander 1830
O. frechi Wysogorsky 1900
O. freija Öpik 1930
O. kuckersiana Wysogorsky 1900
O. orthambonites Verneuil
O. ovata Pander 1830
O. playfairi Reed 1917
O. rotunda Pander 1830
O. sadewitzensis Roemer
O. schmidtii Wysogorsky 1900
O. semicircularis Pander 1830
O. subplicata Reed 1917
O. tetragona Pander 1830
O. transversa Pander 1830
O. umbo Lindström
Orthambonites crassica Pander 1830
O. rotundata Pander 1830

DISCUSSION.—The long known genus *Orthis*, until Hall and Clarke revised it in 1892, was the dump box for all orthid-like forms. We here further restrict the genus to forms agreeing with its genotype. Hence *Orthis* is specially distinguished externally by its strong, rounded, simple costæ which are covered by parvicostellæ, and by the short curved interarea of the ventral valve, which has produced a curved beak. Internally the musculature of the ventral valve and the short, blunt (?) brachioophores of the dorsal valve are characteristic. *Orthis s. s.* may be confused with *Nicolella*, but there are certain external features of the latter which will distinguish the two genera. In the first place, the costæ of *Nicolella* are subangular and covered by concentric growth-lines, and parvicostellæ have never been observed. Furthermore, *Nicolella* has chilidial plates, but in *Orthis* there have been noticed no modifications of either the delthyrium or notothyrium.

Orthis s. s. differs noticeably from American shells referred to this genus by Hall and Clarke, which are here called *Hesperorthis*. In contrast to the short curved interarea of *Orthis* is the long, nearly plane interarea of *Hesperorthis*. Along with the long interarea of the American genus go the receding dental plates. In *Orthis*, on the other hand, the dental plates are continued directly to the floor of the valve. Another more striking difference between the European and American forms is the presence of a short flat deltidium and chilidium in the latter. Such structures have not been observed either directly or indirectly in the European species. Add to the differences already mentioned the variations in the dorsal valve of the European species, and it will be seen that the American genus is decidedly different. The dorsal interior of the American *Hesperorthis* is characterized by long, pointed brachioophores, a cardinal process not

uncommonly cleft antero-ventrally, a larger muscle field, and some variation in the pallial markings.

The internal features of *Orthis s. s.* show relationship to *Billingsella* and *Eoorthis* in the ventral musculature and pallial impressions, and in the cardinalia. In the pallial impressions of most of the Orthacea, the two main trunks given off from the anterior ends of the diductor scars are preserved. This is true in *Orthis s. s.*, but instead of the trunks diverging widely as in *Billingsella*, they are convergent, being separated only by a narrow ridge near the middle of the valve. The pattern of the pallial sinus of the dorsal valve of *Billingsella* and *Eoorthis* is too imperfectly known to make comparison with *Orthis s. s.* possible.

In the dorsal valves of *Billingsella* and *Orthis* the structures of the cardinalia are very close. The brachioophores of both are blunt and short, the cardinal processes are low septa, and the sockets are pits between the outer face of the brachioophore and the wall of the valve. The median ridge in both genera is primitive, being merely a low, broad undulation corresponding to a faint external sulcus. There is little to differentiate the two genera on the basis of the cardinalia, except the more advanced character of those of *Orthis s. s.* There is thus an obvious relationship, more or less remote, between *Orthis*, *Billingsella*, and *Eoorthis*. The variation in the ventral pallial sinus impressions and the presence of a deltidium and chilidium in *Billingsella* are, however, very fundamental differences.

Hall and Clarke typified their restricted group *Orthis* as the group of *O. callactis* Dalman. In so doing they merely designated a body of shells within the genus *Orthis sensu lato*, but did not state definitely that they selected *O. callactis* as the type of the genus. Furthermore, in their definition they obviously employed American shells, and in no sense did they define any group typified by *O. callactis* Dalman. Later Schuchert³⁴ selected *O. calligramma* Dalman as the type of the genus. But before him Davidson³⁵ had already defined the type of *Orthis* as *O. callactis*. This is the first mention of a genotype and the designation is definite, and must stand.

It may be a shock to American paleontologists to have their cherished conceptions of *Orthis* once more upset, but it is clear that this genus as defined by Hall and Clarke was based entirely on American shells, and accordingly their "genus *Orthis*" properly belongs on this side of the Atlantic. However, as Davidson selected the genotype, a common European species, much earlier, we are forced under the rules of nomenclature to accept it, and as the American species are so different from *Orthis s. s.* we must give them a new name, and for this purpose *Hesperorthis*, the "western *Orthis*," seems to be most appropriate.

³⁴ U. S. Geol. Surv., Bull. 87, 1897, p. 282.

³⁵ Brit. Foss. Brach., vol. 1, Introd., 1853, p. 101.

Orthis as here defined has two groups of closely related shells; one, *Orthis s. s.*, typified by *O. callactis* with its flat or concave dorsal valve; and the other, *O. calligramma*, being an example of the biconvex type. It is the former kind of shell that may have given rise to *Nicolella*.

Genus CYRTONOTELLA Schuchert and Cooper 1931

Pl. 2, fig. 14; pl. 4, figs. 1, 4, 5, 11

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 243.

GENIOLOTYPE.—*Orthis semicircularis* (Eichwald) 1829, Zool. Spec., vol. 1, p. 276, pl. 4, fig. 10.

DESCRIPTION. *Exterior.*—Semielliptical, anterior margin rounded, lateral margins straight or concave, hinge-line wide and straight; cardinal angles a right angle or acute. Lateral profile concavo-convex; anterior commissure rectimarginate. Ventral valve strongly convex, interarea short, curved, anacline, ventral umbo strongly convex, beak curved, delthyrium open, wider than long, beak frequently resorbed. Dorsal valve concave, interarea short, plane or slightly curved, anacline to hypercline; notothyrium partially closed by the cardinal process. Ornamentation multicostellate, interspaces with concentric growth-lines. Test impunctate.

Ventral interior.—Delthyrial cavity deep, teeth small; dental plates very widely divergent, thick, overhung by the palintrope, receding; muscle field wider than long, arrangement of the muscles as in *Orthis s. s.* Large pedicle callist in apex. Anterior and lateral margins crenulated.

Dorsal interior.—Notothyrial cavity shallow; brachio-phores short, widely divergent, sockets small; cardinal process a stout ridge projecting above the surface of the interarea; from the notothyrial platform a low ridge extends forward to the center of the shell. Adductor field small, individual components not recognizable; pallial sinuses four in number, sent off from the anterior margins of the muscle area. One pair extends antero-laterally and the other anteriorly, but both die out before reaching the margins of the shell.

GEOLOGIC RANGE.—Middle Ordovician (Echinosphaerites limestone to Wesenberg) of Europe.

SPECIES

Orthis semicircularis (Eichwald) 1829

O. concava Schmidt

DISCUSSION.—*Cyrtotonotella* differs externally from *Orthis* in its multicostellate exterior. The ventral muscle area is much more transverse and the plates less prominent as a result of the strong curvature of the ventral umbo. The ventral pallial sinuses and ovarian impressions are essentially the same as in *Orthis*. In the dorsal valve the pallial markings are

like those of *O. æqualis* but the cardinalia are much less robust. This group is therefore separated from *Orthis* because of the character of the ornamentation and the peculiar profile of the shell.

Genus NICOLELLA Reed 1917

Pl. 2, figs. 1-6

Reed, Trans. Roy. Soc. Edinburgh, vol. 51, pt. 4, 1917, p. 860, pl. 10, figs. 25-27.

GENIOLOTYPE.—*Orthis actoniae* Sowerby 1839, Sil. Syst., p. 639, pl. 20, fig. 16.

DESCRIPTION. *Exterior.*—Semielliptical to semicircular; hinge-line wide and straight, not uncommonly wider than the greatest width of the shell; cardinal extremities acute, drawn out; lateral profile plano- to concavo-convex; anterior commissure broadly sulcate. Ventral interarea very short, curved, orthocline to faintly anacline, umbo swollen, beak strongly curved, delthyrium open; beak commonly resorbed. Dorsal interarea nearly equal in length to the ventral interarea or slightly shorter, anacline to hypercline, notothyrium frequently partially covered by chilidia. Ornamentation paucicostate to multicostate, costæ angular, concentric growth-lines and growth-lamellæ covering the entire surface. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity moderately deep; teeth strong; crural fossettes very deep; dental plates strong and defined by shallow umbonal cavities in young specimens, nearly obsolete in adults; muscle field subcircular; diductor scars subtriangular; adductor scars occupying a central linear track.

Dorsal interior.—Notothyrial cavity obsolete; cardinalia feebly developed, greatly obscured by subsequent shell growth in adults or old individuals; brachio-phores short, small and widely divergent; sockets small; cardinal process lanceolate; chilidia arising between the margin of the brachio-phores and the cardinal process. Median ridge thick, extending to the middle of the valve; dorsal muscle field small; pallial markings not observed.

GEOLOGIC RANGE.—Middle Ordovician (Kuckers to Lyckholm) of Europe and North America.

EUROPEAN SPECIES

N. asteroidea Reed 1917

N. demissa Hisinger 1837

N. rudis Lindström

N. salme Öpik 1930

Orthis actoniae Sowerby 1839

O. moneta Eichwald 1837

O. unguis Sowerby 1839

Productus hamatus Pander 1830

P. pterygoideus Pander 1830

P. striatus Pander 1830

AMERICAN SPECIES

N. agülera Willard 1928

DISTINGUISHING CHARACTERS.—*Nicolella* is characterized externally by its strong angular or subangular costæ, which are simple or may have secondary interpolated costæ in the interspaces; the plano- or concavo-convex profile; the alate or subalate hinge-line; and the chilidial plates that partially close the notothyrium.

Internally it is very similar to *Orthis s. s.* in the ventral musculature and in the development of the dental plates. As in most shells with curved, short palintropes, the fronts of the dental plates extend nearly vertically to the floor of the valve, enclosing a rather deep delthyrial cavity. The muscular pattern of the ventral valve is essentially the same as in *Orthis s. s.* The diductor-adjustor scars are triangular in outline and the position of the adductor muscles is represented by a narrow linear track. Pallial markings were not impressed in any of the specimens studied.

Inside the dorsal valve the most significant variation from *Orthis s. s.* is in the shortness and bluntness of the brachiophores. This variation is without doubt due to the concave growth of the dorsal valve, which makes the brachiophores project almost vertically in a ventral direction. It is not uncommon that much adventitious shell substance is deposited about the brachiophores for their support. The brachiophores, because of their brevity and bluntness, resemble those of *Billingsella* to a marked degree.

DISCUSSION.—Wysogorsky³⁶ gave the origin of *N. actoniæ* (Sow.) as out of *Orthis moneta* Eichwald. It is not, however, *O. moneta* of Eichwald that Wysogorsky figures, but that form as interpreted by Verneuil, which is undoubtedly a new species close to *N. pterygoidea* (Pander). It is evident that *N. actoniæ* and the later *Nicolellas* are descended from *N. pterygoidea* and that type of shell in the early Ordovician. It is doubtful, however, if *Nicolella* arose from *O. calligramma* Dalman, which Lamansky says is restricted to stage B.³⁷ The ancestor of *Nicolella* must be sought in the Ozarkian and will undoubtedly be a billingselloid or eoorthoid form. The chilidial plates of *Nicolella* are probable billingselloid inheritances.

O. callactis Dalman has a very close resemblance in profile and outline to *Nicolella*, but differs in details of ribbing, the former having a predominantly radial ornamentation, costæ and interspaces alike being covered by parvicostellæ. Such fine radial ornamentation has never been observed in *Nicolella*.

The greatest development of *Nicolella* is in the Baltic region of Europe and chiefly in Estonia and Russia. In North America the genus is represented by the single species *N. agilera* Willard. This distribution of *Nicolella* is parallel to that of *Orthis s. s.*, which is represented in North America only by *O. panderiana* Hall and Clarke and *O. buttsi* Schuchert and Cooper.

Genus GLOSSORTHIS Öpik 1930

Pl. 4, figs. 2, 7-9, 12, 28; also figs. 3, 6, 10

Öpik, Acta et Comm. Univ. Tartuensis, A, vol. XVII, pt. 1, 1930, p. 82, pl. 3, figs. 26-33, t. fig. 9.

GENOHOLOTYPE.—*G. tacens* Öpik 1930.

DESCRIPTION. *Exterior.*—Subquadrate in outline; hinge-line straight, narrower than the widest part or forming the widest part of the shell; cardinal extremities acute or obtuse. Lateral profile unequally biconvex, ventral valve with the greater convexity. Anterior commissure rectimarginate. Ventral palintrope the longer, faintly apsacline or orthocline, curved, beak strongly incurved; delthyrium open. Dorsal interarea short, plane, anacline; beak scarcely defined; notothyrium open. Surface costate, costæ angular, rarely bifurcate; interspaces marked by elevated growth-lines or filæ which may or may not be interrupted so as to appear like granules. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep, with marginal thickenings; teeth ponderous, curved, placed laterally of the delthyrial margins. Crural fossettes deep. Dental plates sharply defined, slightly divergent, attached directly to the floor of the valve. Umbonal cavities deep. Muscular area elongate; adductor field linear, elevated, and prolonged into a tongue-like process that extends in front of the diductor scars. The latter are narrow, elongate, attached also on the sides of the dental plates. Adjustor scars not observed. The front margin is crenulated as in other Orthidæ by short ribs corresponding to the external striæ (interspaces), each internal rib bearing a groove.

Dorsal interior.—Notothyrial cavity deep; brachiophores orthoid, blunt, rather short. Cardinal process a linear ridge thickened on its ventral edge. Adventitious shell forming a prominent notothyrial platform and supporting the brachiophores. Muscle area confined; posterior adductor impressions short; anterior pair the larger, each divisible into an inner and outer element as in *Productorthis*. Median ridge extending to the front margin of the adductor field.

GEOLOGIC RANGE.—Middle Ordovician (Walchow, B₂ to Kuckers, C₂) of Europe.

SPECIES

Glossorthis linda Öpik 1930

G. linda virgata Öpik 1930

G. tacens Öpik 1930

Orthis extensa Verneuil non Pander³⁸

³⁶ Zeit. deut. geol. Gesell., vol. 52, pt. 2, 1900, pl. 8.

³⁷ Mém. Com. Géol., n. ser., livr. 20, 1905, p. 176.

³⁸ The species referred to is figured in Geology of Russia, vol. 2, pl. 13, fig. 11a-c. This has nothing to do with *Orthis extensa* (Pander), which belongs to *Panderina*.

DISCUSSION.—The tongue-like process in the ventral musculature of *Glossorthis* is its most characteristic variation from *Orthis s. s.* Opik reports a spondylium in the ventral valve, but in reality the structure is a fine example of a pseudospondylium. As with other brachiopod genera, the anterior part of the floor of the delthyrial cavity may become so thickened by the deposition of callus under the muscles as to form a muscle platform. The callus also spreads upon the sides of the dental plates as a wash, making the ensemble structure appear as a spondylium. In an old example of this genus kindly sent to Schuchert by Opik these phenomena are exhibited to perfection. The front part of the pseudospondylium is composed of adventitious shell, with an elevated marginal rim around the diductor scars. Traced backward, these rims can be followed just beyond the front margins of the dental plates, where they die out. The dental plates extend outside the adventitious material to the base of the valve. The tongue-like feature is evident on young shells but more rapid shell deposit under the adductor scars emphasizes it. Such a pseudospondylium occurs also in our genus *Linoporella*.

Another feature of considerable importance well exhibited in *Glossorthis* is "deltidial plates" (see pl. 4, fig. 28). The teeth are set far outside of the delthyrial margins and there is a line of growth visible on the interarea, showing their progressive forward movement. But on the inside end of the tooth there is another suture line extending to the apex and marking the line of junction of a marginal plate with the inner wall of the delthyrium. It is these marginal plates that limit the delthyrium and produce the shelves of the palintrope which overhang the delthyrial cavity. Similar structures are known in *Ptychopleurella* and *Hesperorthis*.

In the dorsal valve the most interesting anatomical features of the genus center about the cardinal process. It is thin and bladelike, thickened on its ventral edge. The thinning is due, evidently, to attachment of muscles on its sides. Pits on the sides of the notothyrium and floor of the notothyrial platform suggest muscle attachments in these places also, as in other members of the Orthidæ.

Opik believed that *Glossorthis* showed relationships with *Platystrophia*, but a study of the cardinalia and brachiophores at once reveals its intimate relationship with *Orthis s. s.* and its allies.

Genus PAURORTHIS Schuchert and Cooper 1931

(Gr. *pauros*, small)
Pl. 3, figs. 5-8, 10

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 243.

GENOHOLOTYPE.—*Orthambonites parva* Pander 1830, Geogn. Russlands, p. 83, pl. 26, fig. 10a-c.

DESCRIPTION. *Exterior.*—Shell small, dalmanelli-form, subcircular, cardinal extremities rounded; hinge-line straight, shorter than the greatest width; lateral profile subequally biconvex, the ventral valve having the greater convexity; lateral commissure straight or ventrally flexed anteriorly; anterior commissure rectimarginate in young shells but broadly sulcate in adult forms; dorsal sulcus shallow, but pronounced. Ventral interarea short, faintly apsacline to orthocline, curved; ventral umbo swollen, beak strongly curved, delthyrium open, beak not uncommonly resorbed to allow the passage of the pedicle. Dorsal interarea shorter than the ventral, faintly anacline, umbo gently convex, sulcate; notothyrium open. Ornamentation fascicostellate. Test fibrous, impunctate. Exterior layer pierced by pits or exopunctæ.

Ventral interior.—Delthyrial cavity deep; teeth strong, crural fossettes deep; dental plates strong in youthful shells, but obsolete in adult specimens, extending vertically to the floor of the valve; muscle area deeply impressed, slightly elevated in front, longer than wide, occupying about one-third the length and one-fourth the width of the shell. Adductor and diductor impressions not divisible, forming a wide track in the center of the delthyrial cavity and occupying nearly its whole width; adjustor (?) scars located on the sides of the delthyrial cavity. In front of the muscle area a broad or narrow median ridge extends forward nearly to the anterior margin, dividing the ovarian impressions, which are reniform in outline and occupy the lateral spaces of the interior. Anterior margin crenulate.

Dorsal interior.—Notothyrial cavity shallow; brachiophores of the *Orthis* type, being divergent plates placed obliquely to the roof of the valve; extremities subacute; sockets deep, formed by the broad sloping outer face of the crural base and the roof of the valve. Brachiophores supported only by a thickening of the notothyrial platform. Cardinal process a simple, low, linear ridge, or absent; a rounded median septum extending forward from the notothyrial platform to a point slightly beyond one-half the length of the valve. Muscle field small, anterior adductor scars larger than the posterior pair; diductor scars visible on each side of the cardinal process on the notothyrial platform. Ovarian impressions forming two subreniform lobes on the lateral spaces, the anterior ends of the lobes extending only slightly anterior to the front margin of the muscle area.

GEOLOGIC RANGE.—Lower and Middle Ordovician (B1β-B111β) of Europe, and North America.

EUROPEAN SPECIES

Orthambonites parva Pander 1830
O. trigona Pander 1830
Orthis parvula Lamansky 1905
Productus latissimus Pander 1830
P. minimus Pander 1830
P. minutus Pander 1830

AMERICAN SPECIES

Deltatreta elegantula Butts 1926

DISTINGUISHING CHARACTERS.—The chief generic characteristics of *Paurorthis* are the external dalmanellid form combined with a ventral musculature intermediate between that of *Productorthis* and *Orthis*, while the cardinalia have the essential features of those of *Orthis*.

DISCUSSION.—*Paurorthis* externally resembles certain members of the Dalmanellidæ, as *Wattsella* and *Dalmanella*, but is separated easily from these and all other punctate orthids by its impunctate shell. The punctures of the external shell layer of *Paurorthis* must not be confused with the true punctuation of the Dalmanellidæ, which never has any expression on the exterior unless the shell has been abraded. *Paurorthis* differs from *Dalmanella* further in its internal features (compare figs. 5-7 of pl. 3 with figs. 2, 4, 31 of pl. 17). The ventral musculature is closest to that of *Productorthis* in the elevated muscle area and the arrangement of the scars. The cardinalia relate the genus most closely to *Orthis* in the simplicity of the brachio-phores and the cardinal process. In *Paurorthis* the latter is a simple ridge, but in all of the Dalmanellidæ the cardinal process is always multilobate. *Paurorthis* is therefore clearly an *Orthis* that has converged in external form to *Dalmanella*, and in this is an excellent example of homœomorphy.

Paurorthis is also externally similar to *Archæorthis* in the *Dalmanella*-like form and contour but differs internally in the following characters: In the ventral valve of *Paurorthis* there is usually a fairly well defined median ridge, expanded in front, which divides the ovarian impressions. This, however, is not constant in all specimens, some having a rather wide median undulation. In *Archæorthis*, on the other hand, there is no such ridge but the front of the muscle area is extended forward as a lobe formed by adventitious shell. Still more fundamental is the receding character of the dental lamellæ of *Archæorthis* as compared with those of *Paurorthis*, in which the front margins of the plates extend vertically or obliquely forward to meet the floor of the valve. Reniform ovarian impressions were not seen in *Archæorthis*.

In the dorsal valve of *Archæorthis*, the brachio-phores are supported by convergent plates which unite with a short median septum. In *Paurorthis*, on the other hand, the brachio-phores are orthoid in character and supported by a deposit of adventitious shell in the notothyrial cavity, and the median ridge is more prominent and the muscle field wider than in *Archæorthis*.

The exact taxonomic position of *Orthis parva* has long been in doubt. In 1897 Schuchert placed it in the genus *Dalmanella*. This reference was followed by Walcott in the text of his monograph on the Cambrian brachiopods, but when the shell was figured on

his plate 96 it was called *Plectorthis*. Raymond³⁹ places *O. parva* in *Dalmanella* and states that it "is in reality exceedingly punctate," and Walcott figures a thin section showing punctæ (his fig. 10 on p. 99). The junior author examined this section and found that it is not of *O. parva*; it is of a true dalmanellid of the *D. rogata* type, having endopunctæ. In the U. S. National Museum collections there are several specimens of *Dalmanella* s. s. labelled *D. parva* but none of them belongs to *Paurorthis*.

Wysogorsky⁴⁰ was the first to indicate that *O. parva* is actually an impunctate shell, but did not recognize its generic individuality. Recently Kozlowski⁴¹ determined the shell structure of the species but failed to note the character of the punctæ. The experience of the present writers corroborates Wysogorsky's findings that *Paurorthis* as here defined is impunctate but the exterior of the shell is pitted. Thin sections show no endopunctæ. Moreover, the internal structure, musculature, and cardinalia of *Paurorthis* are like those of impunctate *Orthis* s. s., and have no resemblance to similar structures in *Dalmanella*.

Genus ARCHÆORTHIS Schuchert and Cooper 1931

Pl. 6, figs. 7, 8, 16

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 243.

GENOHOLOTYPE.—*Orthis electra* Billings 1862, Pal. Foss., vol. 1, p. 79, fig. 72; p. 217.

DESCRIPTION. *Exterior.*—Shell small, dalmanellid; anterior and lateral margins rounded; cardinal extremities obtuse; hinge-line narrower than the greatest shell width; lateral profile unequally biconvex, the ventral valve usually having the greater convexity; lateral commissure straight; anterior profile unequally biconvex; anterior commissure faintly sulcate. A faint sulcus developed in the dorsal valve. Ventral interarea longer than the dorsal, apsacline, curved, beak slightly incurved, umbo convex; dorsal interarea short, anacline, umbo swollen. Delthyrium open or closed by a deltidium. Ornamentation multicostellate to fascicostellate. Shell structure unknown.

Ventral interior.—Delthyrial cavity deep; teeth strong; crural fossettes very deep; dental plates thick, receding, obsolete in old shells, forming the walls of the delthyrial cavity, but the delthyrial margin is formed by the strongly overhanging edges of the palintrope. The dental plates in young shells are continued forward as a low ridge about the muscle area. The latter is on a callosity that extends from the front of the delthyrial cavity nearly to the middle of the shell.

³⁹ Bull. Mus. Comp. Zool., vol. 66, no. 3, 1916, p. 265.⁴⁰ Zeits. deut. geol. Gesell., vol. 52, pt. 2, 1900, p. 234.⁴¹ Pal. Polonica, vol. 1, 1929, p. 53, footnote.

Diductor scars divergent, elongate, not extending forward of the anterior end of the delthyrial cavity; adductor scars elongate, extended forward to the anterior end of the callosity.

Dorsal interior.—Notothyrial cavity small, moderately deep; cardinalia confined; brachiophores not distinctly separable from the supports; brachiophore supports convergent at their junction with the roof of the valve. A low median ridge extends forward from the anterior ends of the brachiophore supports nearly to the middle of the valve. Cardinal process absent.

GEOLOGIC RANGE.—Ozarkian of North America and Europe.

AMERICAN SPECIES

- Dalmanella electra* (Billings) 1862
D. electra laevis (Matthew) 1893
D. electra major (Matthew) 1893
Orthis euryone Billings ? 1862
O. hippolyte Billings 1862
Eoorthis putillus Walcott 1924

EUROPEAN SPECIES

- Eoorthis christiana* (Kjerulf) 1865
E. daunus (Walcott) 1905
E. tullbergi (Walcott) 1905
E. wimani (Walcott) 1905
 ? *E. bavaria* (Barrande) 1868

DISTINGUISHING CHARACTERS.—The distinguishing characteristics of *Archæorthis* are the dalmanelloid exterior, large ventral muscle area, convergent brachiophore supports, and total absence of a cardinal process.

DISCUSSION.—Through the courtesy of the Canadian Geological Survey it has been possible to study Billings' specimens of *O. electra*, fortunately mostly interiors, but all silicified. Therefore the microstructure of the shell could not be determined. *O. electra* has been referred usually to *Dalmanella* but the internal anatomy does not justify its union with that genus. *Archæorthis* most strongly resembles *Paurorthis* but there are again certain anatomical differences. In the ventral valve the dental plates are much more clearly defined in adult *Archæorthis* than in *Paurorthis*. Furthermore, the latter rarely possesses the callosity in the front of the muscle area, more usually it has a low septal ridge or faint thickening that extends nearly to the front margin of the shell.

In the dorsal valve the chief internal differences lie in the structure of the cardinalia and the absence of a cardinal process. The cardinalia are never so ponderous as in *Paurorthis*, and the brachiophores are not so long. In *Paurorthis* the brachiophores are supported by a swelling of the thickened notothyrial platform around their dorsal edges, but in *Archæorthis* there are thick plates of adventitious shell that converge to the

floor of the valve. The median ridge of *Paurorthis* is much more sharply defined than that of *Archæorthis*. Externally the most notable differences are the lack of marked fasciculation in *Archæorthis* and its less incurved beaks.

Archæorthis is confined apparently to the Lower Ordovician or Ozarkian of America. In this respect it differs also from *Paurorthis*, which appears in the Glauconite sandstone, probably late Lower Ordovician in age, but ranges into the Middle Ordovician (Echinospærites limestone).

Although we are not yet able to point out a satisfactory family relationship for *Archæorthis*, it seems best for the present to range it with the Orthidæ near *Paurorthis*.

Subfamily PRODUCTORTHINÆ Schuchert and Cooper 1931

A small group of aberrant and specialized Orthidæ characterized by exceedingly short interareas or none at all. Both members of the family evolved a productoid form which is carried to perfection in *Productorthis*. The latter is a remarkable example of homœomorphy, foreshadowing a form of shell (but without long tubular spines) that became dominant in the Pennsylvanian and Permian.

Panderina has been placed in association with *Productorthis* because of the great reduction of its interareas; it is clearly developing toward *Productorthis* but internally has not yet reached the latter's stage of high specialization.

Accordingly, this subfamily has the genera *Panderina* Schuchert and Cooper and *Productorthis* Kozłowski.

Genus PANDERINA Schuchert and Cooper 1931

Pl. 3, figs. 1-4

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 243.

GENOHOLOTYPE.—*Productus abscissus* Pander 1830, Beitr. Geogn. Russ. Reiches, p. 86, pl. 27, figs. 7a-c.

DESCRIPTION. *Exterior*.—Subsemielliptical, lateral margins straight or concave; hinge-line straight, cardinal extremities acute. Lateral profile plano- to concavo-convex; anterior commissure broadly sulcate. Ventral interarea extremely short, orthocline, ventral umbo convex or swollen, beak curved, usually resorbed for the passage of the pedicle; dorsal interarea nearly equalling the ventral interarea in length, anacline, notothyrium partially closed by the cardinal process. Ornamentation multicostellate, imbricate in front. There is a tendency in this group for the ventral valve

completely to enclose the dorsal valve anteriorly as in *Productorthis*. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity shallow; teeth small; fossettes moderately deep; dental plates thick and short, continued as a ridge around the front margin of the muscle area, forming a pseudospondylium. Muscle field oval, small, occupying about one-third the length of the valve and less than one-fourth the width. In front of the muscle area is a low median ridge.

Dorsal interior.—Cardinalia confined; crural bases short; cardinal process a thick ridge projecting beyond the level of the interarea; median ridge low, extending to the anterior margin of the muscle field. Muscle area small, anterior adductors the larger, and lobate as in *Productorthis*. Margin crenulated, anterior margin produced into a ridge as in *Productorthis* so that the dorsal valve fits into the ventral valve as an operculum.⁴²

GEOLOGIC RANGE.—Lower Ordovician (B_{1β}-B_{11α}) of Europe.

SPECIES

Productus abscissus Pander 1830

P. abscissus var.

P. extensa Pander 1830

P. latus Lamansky 1905

P. tetragonus Pander 1830

DISCUSSION.—The genus *Panderina* is intermediate between *Orthis s. s.* and *Productorthis*. *Orthis* characters are seen in the short, curved ventral interarea and incurved beak, and the narrow, plane interarea of the dorsal valve. Internally the simple cardinal process shows the genetic connection of the genus. Aberrant characters from *Orthis* toward *Productorthis* are multicostellate exterior and imbrication of the ribs in the anterior of the shell. The strong ventricosity of the ventral valve and the shallowness of the dorsal valve have produced a crenulated flange on the inside of the upper valve which serves to hold the shell firmly in its articulation.

Internally the resemblances to *Productorthis* are a little more remote. The ventral muscle field suggests the latter genus in its elevation on a deposit of adventitious shell and in the short dental plates. An orthoid cardinal process is retained. According to Lamansky's figure there is a suggestion of lobation of the anterior adductors which is a typical *Productorthis* feature.

Panderina appears earliest in the Walchow formations of Lower Ordovician age (B₁) and is one of the oldest of the orthoid genera. Its range extends from B₁ to B_{11α}, where it disappears and *Productorthis* appears for the first time. It is not improbable, then, that *Productorthis* arose from *Panderina*.

Genus *PRODUCTORTHIS* Kozłowski 1927

(An orthid having the form of *Productus*)

Pl. 3, figs. 9, 11-16; pl. 4, figs. 15, 16

Kozłowski, Bibl. Univ. Lib. Polonæ, fasc. 17, 1927, p. 9, pl., figs. 7-9c.

GENOHOLOTYPE.—*Productus obtusus* Pander 1830, Beitr. Geogn. Russ. Reiches, p. 87, pl. 26, figs. 7a-c.

DESCRIPTION. *Exterior*.—Productoid, semicircular to subquadrate; hinge-line long and straight, frequently mucronate; cardinal extremities auriculate; lateral profile concavo-convex to plano-convex to unequally biconvex, the ventral valve always with far greater convexity; anterior commissure rectimarginate or very broadly sulcate. Cardinal interareas absent or remnantal; ventral umbo swollen; beak curved, not uncommonly resorbed for the passage of the pedicle; dorsal beak obsolete; ornamentation multicostellate, rugose, the rugæ being extended as frills. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep, teeth strong; crural fossettes deep; dental plates strong; muscle area borne on a thick platform, longer than wide; adductor and diductor scars not separable; adjustor impressions (?) situated at the base of the dental plates, small and elongate; pedicle callist a small scar in the apex. Posterior margin grooved to form a ginglymoid joint into which the posterior margin of the dorsal valve is inserted; anterior margin crenulate.

Dorsal interior.—Cardinalia confined to the posterior margin; brachiophores short, of the *Orthis* type, supported by a deposit of shell substance under their anterior extremity. This deposit encloses the anterior of the socket so that the crural bases appear to be spoon-shaped. Sockets long and deep. Cardinal process elongate, extending behind the posterior margin. It has a stout, long shaft and thin carinate myophore on its postero-dorsal face. The myophore may be covered by a small circular plate, probably a modified chilidium. A prominent median ridge extends forward nearly to the anterior margin of the lobate muscle area; anterior adductors the larger, each scar being divisible into a smaller and a larger unit; posterior adductors very small, subrectangular, separated from the anterior pair by a low ridge at right angles to the median ridge. Anterior margin thickened to form a dorsally crenulate flange in order to fit into the ventral valve.

GEOLOGIC RANGE.—Lower Middle Ordovician of Europe and South America.

EUROPEAN SPECIES.—The following species of Pander's *Productus* (1830) belong here, together with two other species described by later authors:

Productus aculeatus

P. brevis

P. costatus

⁴² Description of dorsal interior drawn from figures in Lamansky, Mém. Com. Géol., n. s., livr. 20, 1905, pl. 2, fig. 12.

P. eminens
P. intermedius
P. latus
P. obtusus
P. oratus
P. parallelus
P. cf. plana
P. planissimus
P. quinqueradiatus
P. tenuis
Productorthis kayseri Kozłowski 1927 (South America)
 ? *Orthis incurvata* Lamansky 1905

DISCUSSION.—*Productorthis* is the most unique and distinctive of all the Orthacea, being remarkable for its convergence in external form toward *Productus*, but always lacking the spines of the latter. The productoid characteristics are developed to such a marked degree that Pander described many species of this group under the generic term *Productus*. However, Von Buch and De Verneuil showed the true orthoid characters of these shells and placed them in the genus *Orthis*, where they remained until recently, when Kozłowski perceived their uniqueness and separated them from the other orthids under the present designation.

According to Kozłowski, the most important feature of *Productorthis* is the loss of the interareas and the delthyrium, both of which are diagnostic characters of the Orthacea. In this connection it is interesting to note that another group of orthids has also lost the interareas, namely, *Rhipidomella dubia*, which we are referring to our new genus *Perditocardinia*. But here the suppression of the interarea has taken place by lateral compression, producing a rostrate shell when the reduction is complete. In *Productorthis*, however, the hinge-line retains its width and the reduction of the interareas takes place by the shortening of their length.

The reduction of the interareas and the marked ventricosity of the shell in *Productorthis* have produced important changes in the ventral interior, best seen in deviations of the musculature and cardinalia from the usual type in *Orthis*. In the ventral valve of the former, only two sets of muscle-scars are visible, a wide central track which Kozłowski believes represents the adductor impressions and a small scar at the base of each dental plate which he considers to be the diductor scars. This disproportionate size of the two sets of muscles is contrary to any arrangement observed in other orthids in the collections studied. It is the writers' view that the wide central track really represents the adductors and the diductors which can not be differentiated into their component parts. Such a condition is seen also in the genus *Platystrophia*. The small scars at the base of the dental plates of *Productorthis* are interpreted by us as the adjustor scars, since such muscles are commonly seen in other genera of the Orthacea and are always situated at the base or partially on the sides of the dental plates.

Kozłowski believes that the reduction of the interareas and the delthyrium has led to the disappearance of the pedicle as a functional organ. He says:⁴³

Sa suppression chez les formes qui nous occupent est d'autant plus importante qu'elle entraîne la fermeture du delthyrium et par conséquent la disparition du pédoncule, du moins comme un organe fonctionnel.⁴⁴

According to our observations, however, a pedicle callist is present in the apex of the ventral valve, and it clearly indicates the presence of a pedicle although it does not show whether it was functional or not. The resorption of the beak in many of the specimens studied produces a well marked apical foramen, and clearly indicates that the pedicle, by this abrasion, was functional during the life of the individual.

Disarticulated valves might lead the casual observer into the error of identifying a short interarea on each valve. The error would be produced by the "gouttière cardinale" or ginglymus on the ventral valve into which the cardinal margin of the dorsal valve is inserted. Such a ginglymoid joint is a not unusual feature of many productids and has frequently been erroneously described as a rudimentary interarea. Another feature of *Productorthis* is the crural fossette in the inner face of the dental plates, which Kozłowski interpreted correctly as a socket for the insertion of the ventral edge of the brachiophore. This is the first use of the term and the first recognition of the function of these grooves, although they are almost universal structures throughout the Orthacea.

There are three interesting structures in the dorsal valve. Important among these is the evident presence of six muscle impressions, because of the bipartite character of the anterior adductors (see pl. 3, fig. 11). The latter are very variable as to size and as to the proportionate dimensions of the two components. It is possible that the anterior pair represents two muscles whose scars are somewhat lobate, but the definiteness of the impressions favors the view that there are actually four muscles represented in the anterior impressions. To what set of muscles this extra pair could be assigned is a problem. We may perhaps be guided by King (1850),⁴⁵ who has interpreted the musculature of *Productus* as follows: The anterior four impressions are the adductors and the scars conventionally assigned to the posterior adductors may be the "inferior pedicle muscles" which have no complementary scars in the ventral valve as they were attached to the pedicle. This view would not be in accord with the usual interpretation of the musculature of an orthid but is worthy at least of some consideration.

⁴³ Op. cit., p. 6.

⁴⁴ (Translation) Its suppression among the forms with which we are concerned is the more important in that it involves the closing of the delthyrium and the consequent disappearance of the peduncle at least as a functional organ.

⁴⁵ Mon. Perm. Foss., pp. 74-75 and pl. 19, fig. 4.

The great length of the cardinal process in *Productorthis* is a necessary mechanical adjustment to the great arching of the ventral valve for the manipulation of the shallow dorsal valve. Elongation of the cardinal process is a frequent phenomenon in shells having very strongly arched ventral valves and flattened dorsal ones, as in *Triplesia*, *Chonetes*, *Productus*, *Platyorthis*, etc. In connection with the cardinal process, it is worth while to direct attention here to the presence of the small circular plate which covers the postero-dorsal face of the cardinal process, but its function is unknown to us unless it be regarded as the chilidium.

Kozłowski, in seeking the origin of *Productorthis*, looks, with correctness, to some form of biaregerous *Orthis*, and selects as possible ancestors *Productus transversus* Pander and its variety *Orthis transversa latestriata* Lamansky from horizon B₁₈. Both of these forms are provided with areas but they are greatly reduced. They likewise have simple, direct ribs such as the progenitor of *Productorthis* must have had. So far as the external development of *Productorthis* from *Orthis* is concerned, these forms suggest the passage to *O. incurvata* Lamansky, but since the internal features of these forms are unknown it would seem best to retain for the present the genetic descent noted by Kozłowski. It is clear that *Productorthis* came from some type of *Orthis* provided with interareas, such as *Panderina*, but this ancestor appears to be unknown.

Subfamily ANGUSTICARDINIINÆ Schuchert and
Cooper 1931

Substrate costate Orthidæ apparently evolving toward the rhynchonellids but still retaining interareas on both valves and with more of the orthid characters than of those of the Rhynchonellacea. Delthyrium and notothyrium open. Cardinal process linear.

GEOLOGIC RANGE.—Early Middle Ordovician of western Russia.

Includes only the one genus, *Angusticardinia* Schuchert and Cooper.

Genus ANGUSTICARDINIA Schuchert and
Cooper 1931

(Lat. *angustus*, narrow, and *cardo*, hinge)

Pl. 13, figs. 20-23; t. fig. 17

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 244.

GENOHOLOTYPE. — *Porambonites recta* Pander 1830, Beitr. Geogn. Russ. Reiches, p. 97, pl. 11, figs. 7a-e.

DESCRIPTION. *Exterior.*—Shells rhynchonelloid, with a faint fold and sulcus, margins rounded, hinge-line narrow, cardinal extremities occasionally auriculate. Lateral profile biconvex; lateral commissure straight; anterior commissure faintly uniplicate. Ventral interarea longer than the dorsal but very short and

narrow, faintly apsacline, umbo convex, beak curved, delthyrium open. Dorsal interarea anacline; notothyrium open. Ornamentation paucicostate but with interpolation of costæ along the margins. Test impunctate.

Ventral interior.—Delthyrial cavity deep; teeth small; dental plates strongly developed, extended forward as a thickening around the anterior margin of the muscular area; umbonal cavities deep.

Dorsal interior.—Notothyrial cavity moderately deep; cardinalia confined to the umbonal region; brachiophores short and bluntly pointed, supported by strong plates which converge to meet a median ridge that extends for about one-third the length of the shell; cardinal process a linear ridge not reaching the beak. Adductor field small, quadripartite.



FIG. 17.—Sections showing the dental plates of *Angusticardinia*. These ventral interiors strongly resemble those of *Rhynchotrema plenum* from the Chazy, but differ in having a pronounced interarea. The sections have been cut slightly obliquely. The section on the left is not far from the beak. x 3.

GEOLOGIC RANGE.—Early Middle Ordovician of western Russia, with the species *Porambonites recta* and *P. striata*, both of Pander.

DISTINGUISHING CHARACTERS.—The distinguishing characters of *Angusticardinia* are the very narrow hinge-line, which produces a rhynchonellid outline and profile in the shell, the small ears, paucicostate exterior, and the ensemble suggestive of small *Rhynchotrema increbescens*. On the inside the dental plates are strong, and the structure of the cardinalia is unlike that of any other orthid.

DISCUSSION.—These shells externally resemble the rhynchonellids but differ from the members of that superfamily in the possession of an interarea on each valve, an open delthyrium and notothyrium, and a cardinal process. This is the earliest rhynchonelliform shell known and might, with more complete reduction of the interareas and further narrowing of the hinge-line, have given rise to rhynchonellids. All of the fundamental structures are present for such an evolution.

Angusticardinia reminds one somewhat of *Cyclocælia* among American shells but is older and had an independent origin, probably out of some Russian orthid. Although we are unable to prove this, we still think it best for the present to leave these shells in the family Orthidæ as an independent subfamily. Their evolution may have been into the lamellose Ordovician rhynchonellids embraced in the genus *Rhynchotrema*, as *R. increbescens*, *R. capax*, and *R. perlamellosum*.

Subfamily TAFFIINÆ Schuchert and Cooper 1931

Aberrant Orthidæ having a sub-rafinesquinoid habit, with an orthoid interior. Has the following genera: *Taffia* Ulrich and *Eostrophomena* Walcott.

Genus TAFFIA Ulrich 1926

Pl. 16, fig. 11

Ulrich in Butts, Geol. Surv. Alabama, Special Rept. 14, 1926, p. 99, pl. 18, figs. 13-17 (figs. only).

GENOHOLOTYPE.—*T. planoconvexa* Butts 1926.

DESCRIPTION. *Exterior*.—Rafinesquinoid in outline; lateral profile plano-convex to slightly concavo-convex. Ventral interarea long, slightly apsacline or orthocline; delthyrium closed by a non-perforate deltidium; dorsal interarea anacline; notothyrium closed by a complete chilidium. Surface multicostellate. Shell substance fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth large; dental plates short, obsolete in old shells. Muscle marks confined to the delthyrial cavity. Pallial trunks divergent, not unlike those of *Billingsella*.

Dorsal interior.—Notothyrial cavity shallow; notothyrial platform thick, with or without a simple orthoid cardinal process. Brachiophores as in *Orthis* s. s., short, and supported by the addition of callus spreading from the notothyrial platform.

GEOLOGIC RANGE.—Lower Ordovician or Canadian (Odenville) of Alabama, and British Columbia.

SPECIES

Taffia planoconvexa Butts 1926

Protorthis ionas Walcott 1924

P. porcias Walcott 1924

DISTINGUISHING CHARACTERS.—*Taffia* may be recognized by its rafinesquinoid outline and profile, the prominent imperforate deltidium and complete chilidium, and, inside the dorsal valve, by its similarity to *Orthis* s. s.

DISCUSSION.—Externally and internally *Taffia* appears to be most closely related to *Eostrophomena* of the Lower Ordovician of Europe. The European genus is not well known, but a study of the genotypes does not reveal the presence of a cardinal process. Among the early brachiopods, however, the presence or absence of a simple ridgelike cardinal process seems to be of little taxonomic significance.

Genus EOSTROPHOMENA Walcott 1905

Walcott, Proc. U. S. Nat. Mus., vol. 28, 1905, p. 256; Camb. Brach., 1912, p. 795, pl. 95, figs. 6-6b.

GENOHOLOTYPE.—*E. elegantula* (Walcott) 1905.

DISCUSSION.—Walcott applied this name to small shells with a rafinesquinoid outline and profile. The ventral valve is moderately convex and the dorsal is gently concave. The ventral valve has a low fold

and the dorsal is provided with a low sulcus. The valves are unequally multicostellate, fine costellæ being numerous and concentrated between more elevated, distant coarse ones. A dorsal interior figured by Walcott shows a rather strong median elevation separating a quadripartite adductor field. The divergent ends of the brachiophores are barely visible and evidently they enclosed a fairly elevated notothyrial platform. He describes the cardinal process as "more like that of *Orthothetes* than that of *Strophomena*; it differs from both in being more simple in its construction."

The junior author examined the types of *E. elegantula* in the U. S. National Museum and does not concur with Walcott's conclusion in regard to the cardinal process. His figure (1912, pl. 95, fig. 6b) does not show a cardinal process at all, and the specimen does not show an interarea. The notothyrium is covered by matrix so as to conceal the cardinal process if any be present.

Walcott suggests *Strophomena aurora* Billings as congeneric with *Eostrophomena*, and in this the writers agree. According to Billings, however, this species has a simple orthoid cardinal process, and its only strophomenoid feature is a sparsely granular interior.

The evidence thus points to orthoid affinities for *Eostrophomena* rather than to strophomenoid ones. It is not known if either of the shells placed here had a deltidium or chilidium, but even if such were present they would in themselves not prove this early presence of strophomenoids.

Subfamily HESPERORTHINÆ Schuchert and Cooper 1931

Progressive Orthidæ characterized by a long and wide ventral interarea, subreniform ovarian impressions separated by subparallel pallial sinuses, and a low median ridge. The brachiophores are long and more advanced than in the Orthinæ. Remnants of the primitive deltidium and chilidium are retained in a few forms. Marginal growths on the sides of the open delthyrium are conspicuous and such occur as well in shells having a deltidium.

The subfamily may have arisen in the Eoorthidæ and contains the genera *Hesperorthis* Schuchert and Cooper, *Schizoramma* Foerste, and *Dolerorthis* Schuchert and Cooper.

Genus HESPERORTHIS Schuchert and Cooper 1931

(Gr. *hesperos*, West)

Pl. 4, figs. 13, 14, 17-27, 29; pl. 29, fig. 3

Orthis (pars) Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, pp. 192-194, pl. 5, figs. 5-14.

Hesperorthis Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 244.

GENOHOLOTYPE.—*Orthis tricenaria* Conrad 1843, Proc. Acad. Nat. Sci. Philadelphia, vol. 1, p. 333, as described by Hall and Clarke (1892).

DESCRIPTION. *Exterior*.—Semicircular to semi-elliptical; hinge-line straight; cardinal extremities acutely angular or a right angle. Lateral profile plano- or slightly concavo-convex; anterior commissure recti-marginate or faintly and broadly sulcate. Ventral interarea long, plane or gently curved, apsacline, umbo convex, beak gently curved, delthyrium long and narrow, subtending an angle of 30° or less, partially or completely covered by a deltidium. Dorsal interarea shorter than the ventral, plane, strongly anacline, notothyrium open or partially closed by a complete chilidium. Ornamentation paucicostate, interspaces with parvicostellæ and concentric elevated growth-lines. Test fibrous, impunctate, external surface in some species with distantly spaced, coarse pits.

Ventral interior.—Delthyrial cavity deep; teeth small, crural fossettes shallow, oblique; dental plates receding; margin of the delthyrium formed by the palintrope or median extensions thereof; muscle field subcircular or subcordate; diductor scars subrescenscentic or subtriangular; adductor marks central, lanceolate, not extending anterior to the ends of the diductor impressions; adjustor scars not observed. Two subparallel ridges extend from the ends of the diductor scars nearly to the front of the shell. Between these is a faint ridge extending from the anterior margin of the adductors. In some specimens this is forked at its distal extremity. Ovarian impressions occupy the internal lateral spaces and umbonal cavities, being also visible on the lower (anterior) surface of the palintrope. Ovarian markings separated by subparallel pallial sinuses as in *Orthis s. s.* Anterior margin crenulated, each internal rib being cleft medianly.

Dorsal interior.—Notothyrial cavity shallow; cardinalia confined; brachiophores simple, ventrally carinate, forming the margins of the notothyrial cavity, bearing blunt points from the dorso-distal extremity. Brachiophores unsupported except by the shell substance of the notothyrial platform, which is a prominent posterior thickening of the valve. Cardinal process a simple ridge expanded slightly and not uncommonly cleft anteriorly; a broad median ridge extends from the notothyrial platform to the anterior margin of the muscle area. Muscle area large, anterior adductors triangular, larger than the posterior pair. Ovarian markings occupying the internal lateral spaces. Anterior margin as in the ventral valve.

GEOLOGIC RANGE.—Middle Ordovician (Chazy) to at least the middle of the Upper Silurian.

AMERICAN SPECIES

Orthis apicalis Billings 1865
O. costalis Hall 1847
O. davidsoni Verneuil 1848
O. disparilis Conrad 1843

O. pyramidalis Twenhofel 1928
O. tricenaria Conrad 1843
Billingsella (?) *laurentina* (Billings) 1857

EUROPEAN SPECIES

Orthis inostrantzevi Wysogorsky 1900
O. inostrantzevi ubjaënsis Öpik 1930
O. inostrantzevi viruana Öpik 1930
O. plicata Sowerby 1839

DISCUSSION.—Hall and Clarke in their revision of the American brachiopod genera designated a "Group of *Orthis callactis*" as the restricted *Orthis*. Before them, however, Davidson had selected the European *O. callactis* as the type of the genus. It is clear that the American authors in restricting the current conception of *Orthis* had in mind *O. tricenaria* Conrad of the Black River and Trenton of the eastern and mid-western United States as the genotype. Since there are very important differences between their "European" and "American" groups of "*Orthis*," it is now necessary to designate the latter by a new name, *Hesperorthis*, or the *Orthis* of the West.

Important differences between these two groups are to be found both inside and out. Externally the European *Orthis s. s.* is characterized by a short, strongly curved ventral interarea, incurved beak, and swollen umbo, features seen in the North American forms in only two species, *O. panderiana* and *O. buttsi*, n. name. The American or "western" *Orthis*, on the other hand, is distinct by virtue of its elongate interarea, slightly incurved beak, and gently convex umbo.

The markedly different outside expressions of the two groups have made for certain internal differences. It has been shown already that the dental plates of *Orthis s. s.* are extended ventrally directly to the floor of the valve, bounding rather shallow umbonal cavities, which, in mature and gerontic individuals, may become obsolete by deposition in them of adventitious shell. In *Hesperorthis*, on the other hand, the dental plates, as is usual in shells with long and broad palintropes, are receding, that is, extend as ridges postero-ventrally for some distance before uniting with the floor of the valve. The muscle patterns and pallial impressions in the ventral valves of the two groups are essentially alike, thus indicating their close family connections, and their probable origin in some eoorthoid ancestor.

In the dorsal interiors of the two genera are to be found other significant variations. The brachiophores in *Hesperorthis* are usually more elongate and are drawn out into sharp points distally. Further, the muscle field is larger and the anterior adductor scars are subtriangular.

There is still another, perhaps more striking, difference between these two groups, which is the presence of a partial or a fully developed deltidium and chilidium in the American forms and the total absence of these features in the European shells. The only group of Russian orthids showing any modification of the

delthyrium or notothyrium is the aberrant, probably primitive, *Nicolella*. The ensemble of characters exhibited by each of these two groups of shells therefore makes them distinct, although their surficial resemblances would lead the more casual observer to classify them under the same name.

Hall and Clarke homologized the "apical plate" of *Orthis tricenaria* with that seen in *Spirifer*. They say:⁴⁶

In this group of orthids [the authors here doubtless have reference to the American shells], more frequently than elsewhere, we find a character rarely developed in any stage of growth, viz: the existence of a transverse apical plate in the delthyrium of the pedicle-valve. This is probably homologous to the apical plate of the *Spirifers*, but is wholly distinct in origin from the covering of the delthyrium.

As we see this matter, Hall and Clarke are in error in homologizing the apical plate of *Spirifer* with that of *Orthis tricenaria*. In the latter the apical plate differs from a true deltidium in its lack of convexity, which is the usual condition of the deltidium; it is a flattened arch in the delthyrium with its piers built against the sides of the dental plates, and it is quite likely that the deltidium never attains any great degree of convexity because the palintrope overhangs the margins of the delthyrium for some distance. In *O. tricenaria* this flattened arch is formed in precisely the same position as that of *O. laurentina* Billings, but here it is convex and has never been regarded as anything but a true deltidium, a structure that never would be homologized with the plate in "*Spirifer*." In fact, Hall and Clarke regarded the presence of the convex plate in *O. laurentina* as so significant that they placed the species in the genus *Billingsella*, which has a convex deltidium. Since the plate of *O. tricenaria* is formed in exactly the same way as that of *O. laurentina*, and the internal anatomy of the two species is the same, the writers concluded that the "apical plate" of the former is a true deltidium. On the other hand, the "apical plate" of "*Spirifer*" is not an arch with its piers abutting against the sides of the dental plates; on the contrary, it is, in many genera, a solid callosity filling the apex and not infrequently never rises above the level of the interarea. In *Spirifer* this callosity is clearly for pedicle attachment, but the deltidium may also serve the same function though in the reversed way. Even though the two plates may serve the same function, they are, however, not homologous since they originate in different ways.

In America *Hesperorthis* appears first in the Middle Ordovician (Chazy and Ottosee) and is seen last in the Middle Silurian (Chicotte) of Anticosti. In Europe the genus appears first in *O. inostrantzeffi* Wysogorsky of the later Middle Ordovician (Wierland group, C₁₁B, which is about Black River in age), and ranges into the late Silurian (Wenlock).

Genus SCHIZORAMMA Foerste 1912

Pl. 5, figs. 3, 6, 11, 13, 14, 16; t. fig. 4

Foerste, Bull. Sci. Lab. Denison Univ., vol. 14, 1909, p. 77, pl. 3, figs. 45A, B (as *Schizonema* = homonym); vol. 17, 1912, p. 139.

GENOTYPE.—*Hebertella* (*Schizonema*) *fissistriata* Foerste 1909.

DESCRIPTION. *Exterior*.—Shell semicircular to semielliptical, cardinal angles obtuse, hinge-line straight, lateral profile plano-convex to unequally biconvex; anterior commissure rectimarginate, sulcate, or faintly uniplicate; ventral interarea long, strongly apsacline, delthyrium open or partially closed by the overhanging palintrope or a small deltidium; beak not incurved; dorsal interarea very slightly developed, faintly or moderately anacline, beak very small; ornamentation multicostellate to fascicostellate, with strong elevated growth-lines or filæ, especially in the interspaces.

Ventral interior.—Delthyrial cavity shallow, teeth strong, triangular, placed laterally from the delthyrial margin; dental plates strong, thin, receding; palintrope overhanging the delthyrial cavity and simulating deltidial plates; umbonal cavities deep; muscle area small, obcordate, one-fourth the length of the shell in mature forms; commonly marked by a thickening extending from the base of the dental plates; adductor track narrow, linear, extending to the anterior margin of the muscle area; diductor scars subtriangular, divergent; two pallial trunk sinuses extending from the antero-median edges of the diductors nearly to the anterior margin, and defining reniform ovarian impressions as in *Dolerorthis* and *Hesperorthis*; external striæ impressed on the margin of the shell, each bearing a groove.

Dorsal interior.—Notothyrial cavity shallow, cardinalia confined; brachiophores short, orthoid, margining the notothyrium, somewhat spoon-shaped because of adventitious shell under the ventral edge in front, and bearing the shallow sockets; cardinal process linear, expanded in front; in some specimens there is an elevation on the notothyrial platform on either side of the cardinal process (see pl. 5, fig. 14). A strong broad median septum extends from the cardinalia to the middle of the shell, dividing the muscle-scars; adductor impressions subequal, separated by a thin, obscure ridge at right angles to the median septum. Pallial markings obscure but evidently there are two somewhat curved ones radiating from the front margin of each anterior adductor.

GEOLOGIC RANGE.—Middle Silurian.

AMERICAN SPECIES

Orthostrophia (*Schizoramma*) *fissistriata* (Foerste) 1909
Hebertella (*Schizonema*) *celsa* Foerste 1909
Orthis fasciata Hall 1852
O. fissiplica Roemer 1860
O. nisis Hall and Whitfield 1872

⁴⁶ Pal. N. Y., vol. 8, pt. 1, p. 193.

EUROPEAN SPECIES

S. gotlandica, n. sp.

Orthis calligramma subplicata Reed 1917

O. rigida Davidson 1847

O. (Plectorthis) subfissicosta Reed 1917

DISTINGUISHING CHARACTERS.—The external expression of *Schizoramma* is essentially that of *Hesperorthis* in the contour and profile of the valves and the strongly apsacline, plane interarea. It differs, however, in having costellæ instead of costæ, which in some species are bundled into fascicles. From *Dolerorthis* it differs in not having a convexo-concave profile. Externally *Schizoramma* is also marked by the presence of a distinct sulcus in the dorsal valve, but in some species this is present only in young specimens. In old shells the sulcus develops into a fold anterior to the middle of the valve, as may be seen in *S. gotlandica*, n. sp.

DISCUSSION.—In the United States, the species of *Schizoramma* have been variously referred to *Hebertella* and *Orthostrophia*, and the genus was described by Foerste as a subgroup of *Hebertella*. There is, however, no relationship between *Schizoramma* and *Hebertella* and the kinship between the former and *Orthostrophia* is probably also remote. The plan of the ventral musculature and the structure of the cardinalia preclude the placing of *Schizoramma* with *Hebertella*. The genus finds its best place in the group with *Hesperorthis*, since it is but a modified or aberrant form of that genus. Other internal resemblances with *Hesperorthis* are seen in the plan of the musculature; in the narrow, obscure median ridge; and the kidney-shaped ovarian marks. Inside the dorsal valve the likeness to *Hesperorthis* is not so close, and *Schizoramma* differs in its modified cardinal process, smaller adductors, and shorter brachiophores.

An interesting feature of the dorsal valve of *Schizoramma* is the accessory ridges on the notothyrial platform diverging from the cardinal process. These have been observed in other genera but are of sporadic occurrence among impunctate orthids (in a species of *Hebertella*). Such ridges are, however, quite commonly developed in *Schizophoria*, since in two specimens showing them the cardinal process is reduced to a mere septum, and this may mean that these ridges function for the attachment of muscles in the absence of a large cardinal process.

Schizoramma differs from *Orthostrophia* in not having the convexo-concave profile, the very confined ventral musculature, or the small, elevated muscle field of the dorsal valve. Further, the ventral pallial markings of *Orthostrophia* are more complex, more definitely defined, and more like those of *Mimella* than of *Schizoramma*.

It will be noticed that the writers have referred several European species to this genus, and most of these have been so placed from the literature; *S. rigida*,

however, is represented by good specimens in the Schuchert Collection and clearly belongs in this genus. There may be some doubt about *S. gotlandica*, n. sp., which differs from all other forms of the genus in being transversely semicircular rather than subquadrate. An undescribed transverse species, very close to *S. gotlandica*, is represented by a specimen from the Niagaran of Savannah, Illinois.

Schizoramma gotlandica, n. sp.

Pl. 5, figs. 3, 6

Differs from *Orthis rustica* Sowerby, to which it has usually been referred, in its smaller size, in being more strongly apsacline, and in having a more gently curved interarea and a nearly flat dorsal valve which is rather strongly convex.

GEOLOGIC RANGE.—Silurian of Gotland, Sweden.

Cotypes in Schuchert Collection, Yale University (Cat. No. 228).

Genus DOLERORTHIS Schuchert and Cooper 1931

(Gr. *doleros*, deceptive)

Pl. 5, figs. 10, 12, 15, 17-24

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 244.

GENOHOLOTYPE.—*Orthis interplicata* Foerste 1909, Bull. Sci. Lab. Denison Univ., vol. 14, p. 76, pl. 3, fig. 44.

DESCRIPTION. *Exterior.*—Transversely semielliptical to semicircular, hinge-line wide and straight, cardinal extremities acute or obtuse, lateral profile convexo-concave to unequally biconvex, lateral commissure flexed slightly dorsad; anterior commissure broadly uniplicate. Ventral interarea long, faintly curved, strongly apsacline; beak slightly incurved; umbo gently convex. Dorsal interarea shorter than ventral, plane, varying in position between faintly apsacline and moderately anacline, umbo gently convex; delthyrium and notothyrium open. Ornamentation pauci- to multicostate. Growth filæ strong in the interspaces. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity moderately deep; teeth small; crural fossettes small, oblique; dental plates moderately strong in young shells but nearly obsolete in adults or old specimens, extended as a thickening about the muscle area in some species; muscle area obovate; adductor scars elongate, forming together a lanceolate track; diductor impressions large, subcrescentic; adjustor scars not distinguishable; in most species a faint ridge or septum separates the pallial trunks that branch abruptly near the front margin of the shell. Large subreniform ovarian impressions occupy the lateral spaces and the umbonal cavities. Anterior margin costate, each costa being cleft centrally.

Dorsal interior.—Notothyrial cavity shallow, cardinalia strong; brachiophores strong, broadly rounded in front, of *Orthis* type, and bearing flat, bluntly pointed plates on the outside distal extremity. Cardinal process a simple linear ridge; a median ridge extends from the notothyrial platform to the middle of the shell. Muscle area small; anterior adductors smaller than the posterior ones, irregular; posterior adductor track broad and long. Ovarian impressions occupy the internal lateral spaces as reniform areas.

GEOLOGIC RANGE.—Lower and Middle Silurian.

AMERICAN SPECIES

Orthis flabellites Foerste 1889
O. flabellites dinorthis (Foerste) 1895
O. flabellites euorthis (Foerste) 1895
O. flabellites fissiplicata (Foerste) 1895
O. flabellites militaris Foerste 1909
O. interplicata Foerste 1909
O. nettelrothi Foerste 1909

EUROPEAN SPECIES

Orthis rustica Sowerby 1839
O. rustica osiliensis Schrenk 1858

DISTINGUISHING CHARACTERS.—The characteristics used in separating *Dolerorthis* from other orthid genera are: (1) The convexity of the valves is the reverse of that normally seen in *Orthis s. s.* or *Hesperorthis*; (2) the dorsal valve is similar to that of *Dinorthis* in all but the cardinal process. Family relationships with the Orthidæ are seen in the ventral muscle field, which has a pattern like that of *Orthis s. s.*, and essentially as in *Hesperorthis*. Furthermore, *Dolerorthis* has in the ventral valve the low, narrow, forked median septum, the pallial trunks and reniform ovarian impressions of *Orthis*. In the dorsal valve, affinities with the Orthidæ are seen in the brachiophores.

Dolerorthis is readily distinguished from its subfamily companions, *Hesperorthis* and *Schizorammina*, in having the relative convexity of the valves reversed, but is not resupinate as are the strophomenids. The disproportionate convexity between the two valves, the dorsal being the more convex, is a consequence of this reversion, and brings about the superficial external resemblance to *Dinorthis*. There is, however, a rather marked difference in the cardinal process of *Dinorthis* and *Dolerorthis*, since in the latter genus it is a simple ridge, while in the former it is thicker and the posterior surface is crenulated, showing that the muscle attachments were on this portion of the process and not on its sides or at its base.

DISCUSSION.—*Dolerorthis* is another group of brachiopods showing effectively the disconcerting rôle played by homœomorphy. Within the group are found homœomorphs of *Plæsiomys* and *Dinorthis*. For many years *Orthis flabellites* was mistakenly identified with

O. flabellulum (Sowerby) but in 1867 Hall⁴⁷ changed the name to *flabellites*, and Foerste⁴⁸ did the same in 1889 when he pointed out the anatomical differences. Hall and Clarke⁴⁹ regarded *O. flabellites* as "a form connecting the typical Orthidæ with *Dinorthis*; though, in geological time, appearing at the end of the two groups." Had they realized the presence of homœomorphy they would have recognized at once the uniqueness of *Dolerorthis*. The latter differs from *Dinorthis* in both ventral and dorsal valves, in features which are of family import. In the first place, *Dolerorthis* does not have the quadrate muscle field of the other group, and besides, in *Dinorthis* there are two pallial trunks extending antero-laterally from the diductor scars, which in their passage toward the front break up into numerous subsidiary rami, and there are no kidney-shaped ovarian marks occupying the umbolateral spaces. Again, *Dolerorthis* does not have the crenulated cardinal process. On the other hand, the multicostate species *D. interplicata* and *D. rustica* have a superficial resemblance to some members of *Plæsiomys*, but the homœomorphy in these instances is less striking than that shown by *Orthis flabellites* and *Dinorthis flabellulum*.

It may be well to say here that some of the shells now passing under the name *Orthis flabellites* do not conform with the shells that occur in New York and Indiana in the Middle Silurian. These are of the older Cataract of Ontario, and they are smaller than the type species and are quite clearly biconvex. Like many other "comfortable" species, this one is in sore need of revision in the light of modern paleontology.

Subfamily GLYPTORTHINÆ Schuchert and Cooper 1931

Specialized Orthidæ with the general internal expression of the Hesperorthinæ but with a rugose external surface. Deltidium and chilidium absent. This small family is composed of three closely related genera. *Eridorthis* appears to be a *Glyptorthis* which has accomplished a reversion of the fold and sulcus toward the front of the shell. *Ptychopleurella* is an off-shoot from *Glyptorthis*, with an unusual subspiriferoid contour and profile.

Genus GLYPTORTHIS Foerste 1914

Pl. 5, figs. 4, 7, 8; pl. 6, figs. 12, 17, 18, 20, 21, 26, 29

Foerste, Bull. Sci. Lab. Denison Univ., vol. 17, 1914, p. 258.

GENOHOLOTYPE.—*Orthis insculpta* Hall 1847, Pal. N. Y., vol. 1, p. 125, pl. 32, fig. 12.

⁴⁷ 20th Ann. Rept. N. Y. State Cab., p. 436; see also Paleontology of New York, vol. 8, pt. 1, p. 227.

⁴⁸ Proc. Boston Soc. Nat. Hist., vol. 24, p. 311.

⁴⁹ Pal. N. Y., vol. 8, pt. 1, p. 227.

DESCRIPTION. *Exterior.*—Shell small or large, subquadrate, semielliptical, anterior margin convex, commonly slightly emarginate, hinge-line wide and straight, cardinal angles straight or obtuse, occasionally subauriculate; lateral profile unequally biconvex, the dorsal valve being the more convex; anterior commissure sulcate; ventral fold very low; dorsal sulcus deep; ventral interarea orthocline to catacline, curved or plane, delthyrium open, beak incurved; dorsal interarea curved, orthocline to apsacline, narrow, beak slightly incurved or straight; ornamentation multicostate or costate, crossed by strong imbrices which are not uncommonly produced into frills. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity moderately deep, teeth strong, crural fossettes oblique, interarea overhanging the dental plates and not infrequently narrowing the delthyrium considerably; dental plates strong in young shells, but obsolete in old ones; muscle area obcordate, strongly impressed, elevated somewhat anteriorly; adductor track broad, central, commonly elevated, nearly equal to or greater than the diductor impressions in length and width; diductor scars narrow, divergent, elongate; adjustor impressions narrow, elongate, at base of dental plates. Pallial markings orthoid; two reniform ovarian areas marked by radiating elevated lines occur on each side of the muscle area. A short median elevation extends from the adductors for more than half the distance to the margin, expanding in front. Anterior and lateral margins costellate.

Dorsal interior.—Notothyrial cavity shallow, cardinalia strong; brachiophores orthoid, forming the margins of the notothyrium, supported by adventitious shell substance of the notothyrial platform; cardinal process a thickened linear ridge, bearing the diductor impressions on the lateral surfaces; notothyrial platform thickened, produced forward as a median ridge at least to the middle of the valve; posterior adductor scars smaller than the anterior pair, separated from them by an arched ridge at right angles to ventrally oblique to the median one. Pallial markings consisting of the usual two pairs of curved trunks from the anterior end of the median ridge, with the addition of two trunks from the outside of the anterior adductors.

GEOLOGIC RANGE.—Early Middle Ordovician (Ridley of Stones River) to Upper Ordovician (Richmond).

AMERICAN SPECIES

- Dalmanella crispata* (Emmons) 1842
Glyptorthis insculpta manitoulinensis Foerste 1924
Hebertella bellarugosa (Conrad) 1843
H. daytonensis (Foerste) 1885
H. fausta (Foerste) 1885
H. insculpta (Hall) 1847

EUROPEAN SPECIES

- Orthis balclatchiensis* Davidson 1883
O. crispa McCoy 1846

DISCUSSION.—This group of orthids has ordinarily been identified with *Hebertella*, but, as pointed out by Foerste in 1914, *Orthis insculpta* and its allies are totally distinct from that genus and belong in his new genus *Glyptorthis*. The chief difference pointed out by him between the two genera is the lamellose exterior of *Glyptorthis*. He also indicated that there was a tendency for the dorsal valve of *Glyptorthis* to be sulcate, whereas the corresponding valve of *Hebertella* shows a prevalent tendency toward the development of a fold. He concludes:

In both groups, there are forms in which the median part of the brachial valve is more or less strongly depressed, so as to produce a median sinus, so that the chief distinction of the *Hebertella insculpta* group is, after all, the presence of the concentric lamellose lines of growth, combined with a shell form which otherwise agrees with that of *Hebertella*.

According to our views, *Glyptorthis* differs from *Hebertella* in certain features that are far more fundamental than the imbrication of the growth lamellæ. The internal structures at once relate the genus to *Orthis* and *Hesperorthis* rather than to *Hebertella*, and between them the chief differences are as follows: (1) Externally *Glyptorthis* is always provided with a sulcus in the dorsal valve, a feature not common among orthids. In *Hebertella*, on the other hand, this feature is characterized by its instability, a fold or sulcus being developed on the dorsal valve in certain species and more uncommonly either one or the other occurs in the same species.

(2) Internally the ventral valve of *Glyptorthis* varies importantly from that of *Hebertella* in its musculature and in its pallial markings, and in these features there is also seen the clue to the taxonomic position of the former. The ventral musculature is characterized by the presence of a full complement of muscle-scars, the adjustors being in position at the base of the dental lamellæ, but the presence of these muscles in *Glyptorthis* is a feature not usually seen in the Orthidæ. It is probable that in other members of this family the adjustors are joined with the diductors and do not register their presence as a scar on the floor of the valve, or again, they may occupy the sides of the dental plates and therefore have escaped attention. At any rate, they are clearly visible in *Glyptorthis* and have not been definitely located in *Hebertella*, in which the diductor scars are expanded in front and the position of the adductor is represented by a double-tracked ridge upon which are attached the lanceolate adductor scars. This is a considerable variation from the condition seen in *Glyptorthis*, in which the diductor scars are attenuated in front and rather narrow throughout, and the adductor track is linear, rather flat, and expands anteriorly. In front of the adductor track in *Glyptorthis* is a narrow median ridge which expands exactly as in *Orthis s. s.*, *Paurorthis*, *Hesperorthis*, *Dolerorthis*, etc. The prominent kidney-shaped ovarian impressions of *Glyptorthis* are striking features of this genus and are never seen in *Hebertella*.

Generic and family differences distinguishing *Hebertella* from *Glyptorthis* are to be found in the dorsal valves. The brachiophores, and especially the cardinal process of the last named genus, are of the orthoid type. In *Hebertella*, on the other hand, the cardinalia are composed of brachiophores intimately combined with distinct convergent supporting plates which unite with the floor of the valve at the base of the cardinal process, while in *Glyptorthis* the orthoid brachiophores are supported by adventitious shell deposited in the notothyrial cavity, as in all other Orthidæ. Rather deep adductor pits and the scars of attachment of one set of the diductors at the base of the cardinal process have so excavated the notothyrial platform as to make it simulate the condition seen in *Hebertella*.

The pallial markings in the dorsal valve of *Glyptorthis* vary from the simple markings of *Orthis* s. s. and *Cyrtionotella*. In the former the four trunks are given off from the anterior ends of the diductors but are bifurcated at their inception. Subsidiary rami are developed along the front margins.

Glyptorthis first appears in the early Middle Ordovician (Ridley member of the Stones River) in Kentucky and Tennessee, and ranges into the Richmond division of the Upper Ordovician. In the Girvan district of Scotland the genus appears first in the Stinchar limestone (= Chazy) and ranges into the Drummock group (= Richmond).

Genus ERIDORTHIS Foerste 1909

Pl. 5, figs. 1, 2, 5, 9

Foerste, Bull. Sci. Lab. Denison Univ., vol. 14, 1909, p. 223, pl. 4, figs. 3a-d.

GENOLECTOTYPE (Schuchert and LeVene 1929).—*Plectorthis* (*Eridorthis*) *nicklesi* Foerste 1909.

DESCRIPTION. *Exterior*.—Very similar in general physiognomy to *Glyptorthis*, but varying in important details. Outline semicircular, cardinal extremities obtuse or rounded, slightly deflected; lateral profile commonly subequally biconvex, with the ventral valve usually slightly more convex; in young shells there is a median fold on the ventral valve and a sulcus on the dorsal, but in mature individuals the latter becomes a more or less prominent fold, while the fold of the opposite valve is anteriorly depressed. Ventral interarea the higher, curved and strongly apsacline, umbo convex. Dorsal interarea short, apsacline, notothyrium open. Ornamentation multicostate, with prominent concentric lamellæ as in *Glyptorthis*. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity shallow; teeth strong; dental plates well defined in mature shells; muscle area placed on a low callosity, cordate or subtriangular, adductor track linear, expanding anteriorly. Diductor tracks elongate, narrow; adjustor scars narrow when visible. Pallial and ovarian impressions obscure, but when visible, much as in *Glyptorthis*.

Dorsal interior.—Cardinalia very confined; brachiophores of the *Orthis* type, short, blunt, supported by the notothyrial platform; cardinal process a simple linear ridge; median ridge extending about one-half the length of the valve; muscle area small, quadripartite; pallial and ovarian impressions obsolete.

GEOLOGIC RANGE.—Middle Ordovician and early Silurian of North America.

SPECIES

Hebertella (*Eridorthis*) *nicklesi* (Foerste) 1909

H. (E.) rogersensis (Foerste) 1909

DISCUSSION.—Foerste separated this assemblage as a subgeneric group under *Plectorthis* chiefly on the basis of external features. The internal characters, however, show it to have no relationship with *Plectorthis*, but to be related genetically to *Glyptorthis* and the Orthidæ in general. *Eridorthis* differs from the other members of the Glyptorthisinæ chiefly in its external characteristics. The dorsal valves of *Glyptorthis* and *Ptychopleurella* are always marked by a sulcus, but in *Eridorthis* the dorsal sulcus reverts into a fold or is lost in the general convexity of the valve. Externally it differs from *Plectorthis* in the characters of the fold and sulcus and likewise in the rugose ornamentation.

The interior of the ventral valve has *Orthis* characters as seen in the low median ridge, traces of reniform ovarian impressions, and subparallel pallial impressions. The brachiophores and cardinal process are distinctly of the *Orthis* type. These are the most important differences between *Eridorthis* and *Plectorthis* and absolutely preclude the placing of the former as a subgenus of the latter and set it apart in a separate subfamily.

From *Glyptorthis* this genus differs mainly in the reversion of the fold and sulcus and in the lesser development of the ovarian and pallial impressions. *E. nicklesi* and *E. rogersensis* were first referred by Foerste to *Plectorthis*, and later all four of the species were listed by Bassler under *Hebertella*. It must be emphasized, however, that *Eridorthis* has none of the typical features of *Hebertella* as exhibited in the genotype of that genus. The ventral musculature and what traces of the pallial and ovarian markings are present clearly indicate affinities with *Hesperorthis*, *Dolerorthis*, *Schizoramma*, and other genera of the Orthidæ.

Externally, the degree to which the development of fold and sulcus is carried is an important distinguishing characteristic of *Eridorthis*. In the dorsal valve of young shells there is a shallow sulcus bordered by the first radiating costæ. This sulcus may extend for 3-5 mm., and then with the implantation of the first ribs on the inside of the primary marginal costæ, the sulcus becomes an elevated median fascicle. On the ventral valve the median costa is elevated at the beak,

forming a fold in the young shell. This costa continues elevated for some distance in the mature shell, but toward the front a sulcus is developed to correspond to the elevation of the dorsal median fascicle.

Genus PTYCHOPLEURELLA Schuchert and Cooper 1931

(Gr. *ptux*, wrinkle; *pleura*, rib)

Pl. 6, figs. 1-6, 9, 32, 33

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 244.

GENOHOLOTYPE. — *Orthis bouchardi* Davidson 1847, London Geol. Jour., Feb. 1847, p. 64, pl. 13, figs. 5-8.

DESCRIPTION. *Exterior.*—Shells small, subelliptical, ventral valve subpyramidal; anterior margin emarginate, lateral margins convex; hinge-line wide and straight; cardinal extremities obtuse; lateral profile unequally biconvex, the dorsal valve with the greater convexity; anterior commissure sulcate; ventral interarea plane or slightly curved, strongly apsacline to procline, delthyrium open or constricted by lateral plates; dorsal interarea much shorter than the ventral, strongly curved, faintly apsacline to orthocline, notothyrium open, umbo convex, beak fairly well defined, incurved; usually a strong sulcus in the dorsal valve, not uncommonly also in the ventral.

Ornamentation multicostate, but the ribs are very sparse, sharp, and elevated. The whole surface is covered by imbrices which are occasionally produced into short hollow processes. Shell substance impunctate.

Ventral interior.—Delthyrial cavity moderately deep; teeth small, sharp; fossettes oblique; lateral plates overhanging the delthyrial cavity; dental plates nearly obsolete in old shells, muscle area cordate; adductor track elongate, expanded in front, commonly elevated; diductor tracks and scars elongate, narrow; adjustor scars not clearly visible; a small pedicle callist in the apex; pallial and ovarian marks obscure but the traces are similar to those of *Glyptorthis*.

Dorsal interior.—Brachioophores forming the margin of the notothyrial cavity, supported by thick shelving deposits that define the notothyrial platform; cardinal process a linear ridge, with the diductor impressions on its sides; a median ridge extending more than half the length of the shell. Adductor scars small.

GEOLOGIC RANGE.—Middle Ordovician to late Silurian.

AMERICAN SPECIES

Orthis (?) *lamellosa* Twenhofel 1914

O. rugiplicata Hall and Whitfield 1872

Skenidium (?) *nodocostatum* Rowley 1904

Glyptorthis sublamellosa Cooper 1930

Ptychopleurella matapedia, n. sp.

EUROPEAN SPECIES

Orthis bouchardi Davidson 1847

O. keisleyensis Reed

O. lapworthi Davidson 1883

O. ? monticula Salter⁵⁰

DISCUSSION.—This genus comprises small neat shells and is unique for certain external and internal features. Externally it is characterized by the subpyramidal ventral valve and rather strongly convex dorsal valve, which in all of the species is marked by a deep sulcus bounded by two costæ elevated considerably above their fellows. Inside these two primary costæ there are always implanted two secondary ribs near or far from the former according to the species. On the ventral valve there is always a median costa, more or less elevated at the beak but becoming depressed in the shallow sinus toward the front. The sinus is bounded by the two main lateral ribs on each side of the primary costa, and toward the front secondary ones are intercalated.

In the ventral interior the muscle field is elevated, forming a pseudospondylium. The plan of the muscles is essentially the same as that of *Glyptorthis* except that the diductor scars are not so drawn out in front and the adjustor scars are not so well developed. In front of the adductor track there is a remnant of a median ridge as in *Orthis s. s.*, *Hesperorthis*, and *Glyptorthis*. Pallial impressions have not been observed in their entirety and their reduction is a variation from *Glyptorthis*. The brachioophores and cardinal process are orthoid, and the muscle field is small, quadripartite. The posterior adductor scars are very small, and almost obsolete in *P. bouchardi* and *P. rugiplicata*.

According to Davidson,⁵¹ the test of *O. bouchardi* is punctate, but the writers were unable to find any punctæ. The constriction of the delthyrium by lateral plates is a feature of the ventral valve worthy of note, and has been seen in several species, especially *P. lamellosa* and *P. sublamellosa*. This reduction of the delthyrium has been carried to such a degree in *P. lamellosa* that it is but a narrow slit. This tendency of shell growth along the margins of the delthyrium has been noticed in several genera, i. e., *Schizoramma* (*S. gotlandica*), *Orthis s. s.*, *Hesperorthis*, etc., and is more fully discussed on page 23. Twenhofel⁵² says of *P. lamellosa*:

Wetting of the ventral area shows that narrow side plates are annexed to the sides of the foramen; these are supposed to be continuous with the teeth, as in *O. bouchardi*, the nearest related species. These plates simulate deltidial plates, with which, however, they are probably in no way homologous.

⁵⁰ Reed, F. R. C., Pal. Indica, ser. XV, vol. 7, no. 2, 1912, pl. 5, figs. 1, 2.

⁵¹ Brit. Foss. Brach., vol. 3, 1866-1871, p. 210.

⁵² Geol. Surv. Canada, Mem. 154, 1927 (1928), p. 176.

Ptychopleurella matapedia, n. sp.

Pl. 6, figs. 2, 5

Shell small, subrectangular, lateral margins nearly straight, anterior margin rounded, probably emarginate. Hinge-line straight, equal to the greatest width of the shell. Anterior commissure sulcate. Ventral valve subpyramidal, interarea long and broad, strongly apsacline, beak not incurved, delthyrium narrow, triangular. Dorsal valve convex, the greatest convexity in the vicinity of the umbo. There are eight primary costæ on the dorsal valve, the middle two elevated above their fellows and defining a deep sulcus. There are nine secondary costæ, two occupying the sulcus. The latter two take their origin about 1 mm. from the beak. Ventral valve provided with eight primary ribs and ten secondaries. The median ridge is depressed below the surface of the ventral sulcus. Each primary rib, except those at the interarea borders, has two implanted parasitical secondary ribs on either side, thus forming fascicles of three ribs. At the front of the shell there are three rugæ to a millimeter.

DIMENSIONS (holotype):

| Length | Width at widest part | Thickness | Width at hinge |
|--------|-------------------------|-----------|-------------------|
| 6 mm. | 8.5 mm. | 4.5 mm. | 8.5 mm. |

The nearest relative of this species is *P. bouchardi*, but the Canadian form differs chiefly in its wider hinge-line, that of *P. bouchardi* being much narrower than the total width of the shell. Other important differences from *P. bouchardi* are seen in the narrower, more elevated ribs and lesser rugæ.

HORIZON AND LOCALITY.—Lower Devonian ? or highest Silurian, 3 miles east of Dawsonville, New Brunswick, on the Upsalquitch road, Quebec, Canada. Holotype, Cat. No. 287, Schuchert Collection, Yale University.

Family DINORTHIDÆ Schuchert and
Cooper 1931

Progressive Orthacea probably derived out of the Orthidæ and having a subquadrate ventral muscle field, *Orthis*-like brachiophores, and a simple cardinal process with a crenulated myophore. A prolific group characteristic of the Ordovician.

The family embraces the following genera:

Dinorthis Hall and Clarke and its subgenera, as follows:

Dinorthis s. s.
Plæsiomys Hall and Clarke
Pionorthis Schuchert and Cooper
Retrorsirostra Schuchert and Cooper
Marionella Bancroft

Valcoura Raymond
Multicostella Schuchert and Cooper
Austinella Foerste
Planidorsa Schuchert and Cooper
? *Palæostrophomena* Hortedahl

DISCUSSION.—Externally most of the Dinorthidæ are convexo-concave in outline and rather easily recognized because of their strophomenoid habit. The ventral muscle field is unique for its very large adjustor scars, the expansion of which makes the subquadrate field so characteristic of the family. A small apical deltidium is not infrequent.

In the dorsal valve the brachiophores are essentially of the *Orthis* type, but the cardinal process is progressive, since it is crenulated on its posterior surface for the attachment of the diductor muscles.

In view of our reduction of *Plæsiomys* to the status of a subgenus of *Dinorthis*, it is no longer desirable to continue the subfamily name *Plæsiomiinæ* of Schuchert 1913⁵³ and his recasting of it in 1929⁵⁴ to include what are now seen to be unrelated genera.

The genetic relations of the Dinorthidæ are thought to be as shown in Table 6.

Genus DINORTHIS Hall and Clarke 1892

Pl. 9, figs. 1-11, 13, 14, 20-23; pl. 10, figs. 15, 17, 18, 24-26; t. figs. 5, 18

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, pp. 195, 222, pl. 5, figs. 27-33.

GENOTYPE. — *Orthis pectinella* Emmons 1842, Geol. N. Y., Rept. 2d Dist., p. 394, fig. 2.

This genus is here divided into five subgenera: (1) *Dinorthis s. s.* Hall and Clarke; (2) *Plæsiomys* Hall and Clarke; (3) *Retrorsirostra* Schuchert and Cooper; (4) *Pionorthis* Schuchert and Cooper; (5) *Marionella* Bancroft, which appears to be a parallel development with *Plæsiomys*.

DESCRIPTION (OF DINORTHIS SENSU LATISSIMO). *Exterior*.—Shells transversely semielliptical to subquadrate, lateral profile convexo-concave to unequally biconvex; anterior commissure rectimarginate, faintly sulcate or uniplicate; ventral valve commonly broadly sulcate; dorsal valve frequently sulcate but the depression always narrow and shallow; ventral interarea longer than the dorsal, apsacline; dorsal interarea apsacline or orthocline; delthyrium generally open, but more uncommonly partially closed by a short deltidium; notothyrium partially closed by cardinal process. Ornamentation pauci- to multicostate, and with fine concentric elevated growth-lines and lamellæ of growth. Test fibrous, impunctate, with occasional tubulose costellæ.

⁵³ Zittel-Eastman Text-book of Paleontology, 2d ed., vol. 1, p. 382.

⁵⁴ Foss. Cat., Pars 42, p. 14.

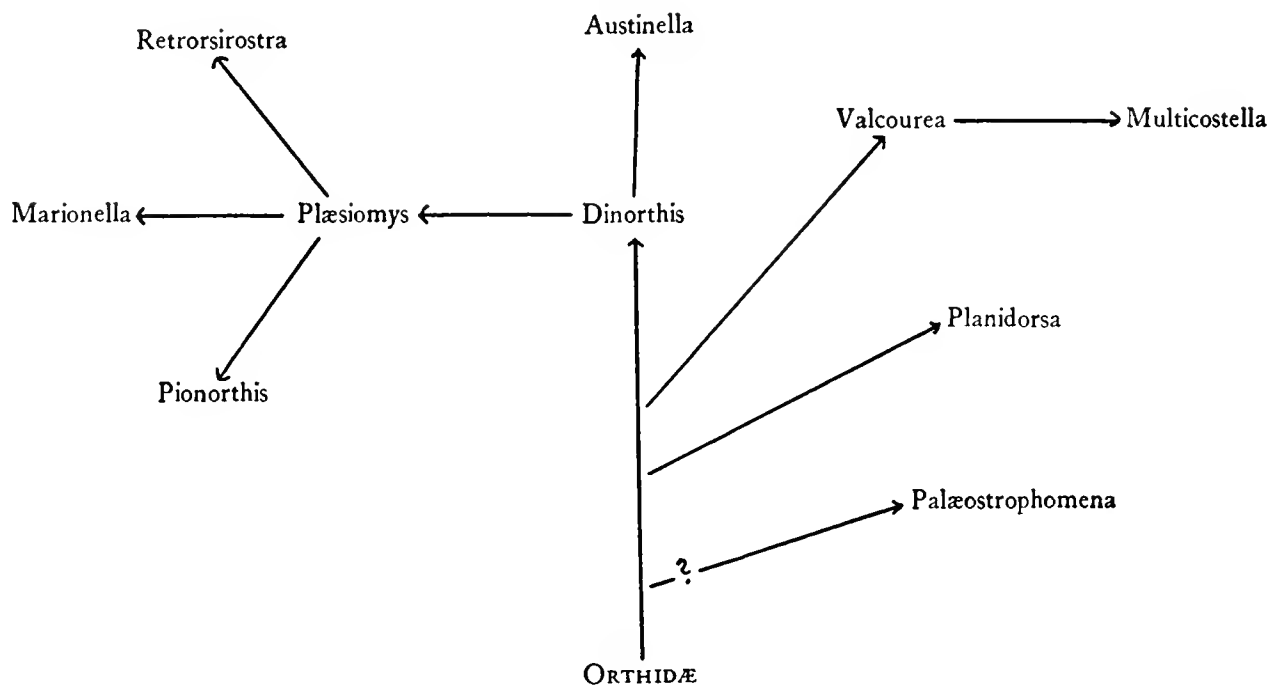
Ventral interior.—Teeth strong, with shallow sockets; crural fossettes oblique; dental plates obscure in old shells, more prominent in young ones, not receding; umbonal cavities shallow; muscle area quadrate in outline, anteriorly bilobed, adductor scars small, the two forming a central oval field divided by a low median elevation; diductor scars diverging, expanded in front, so as to enclose the adductors; adjustor scars prominent, about one-half the length of the diductors; pedicle callist triangular; pallial markings prominent, consisting of two main trunks given off from the

GEOLOGIC RANGE.—Middle and Upper Ordovician (Chazy to Richmond).

AMERICAN SPECIES OF DINORTHIS s. s.

Dinorthis atavoides Willard 1928
D. interstriata Willard 1928
D. pectinella (Emmons) 1842
D. proavita (Winchell and Schuchert) 1892
D. quadruplicata Willard 1928
Orthis semiovalis Hall 1847
O. sweeneyi N. H. Winchell 1881

Table 6



antero-lateral extremities of the diductor scars; these trunks are short and soon bifurcate, sending one subsidiary postero-laterally, the other anteriorly; both of these send off many minor branches. Anterior margin finely crenulate.

Dorsal interior.—Notothyrial cavity shallow; brachio-phores orthoid, diverging, unsupported except by adventitious deposit, bluntly pointed ventro-distally; sockets defined by the sloping outer face of the brachio-phore and an excavation beneath the palintrope; cardinal process strong, crenulated on the postero-ventral face, the crenulation in old shells giving a bilobed appearance; median ridge short, extending less than one-half the length of the shell; posterior adductor scars smaller than the anterior pair, separated, in some specimens, by curved oblique lines at an angle to the median ridge.

FOREIGN SPECIES OF DINORTHIS s. s.

| | |
|---|------------------------------|
| <i>Orthis flabellulum</i> Sowerby 1839 | } Placed from the literature |
| <i>O. (Dinorthis) thakil</i> Salter 1865 | |
| <i>O. (D.) thakil convexa</i> Salter 1865 | |
| <i>O. (D.) thakil trifida</i> Salter 1865 | |
| ? <i>O. (D.) annamitica</i> Mansuy | |

AMERICAN SPECIES OF PLÆSIOMYS

Dinorthis columbia Wilson 1927
D. iphigenia (Billings) 1862
D. meedsi (Winchell and Schuchert) 1892
D. meedsi arctica Schuchert 1900
D. meedsi germana (Winchell and Schuchert) 1892
D. rockymontana Wilson 1927
D. subquadrata (Hall) 1847
D. transversa Willard 1928
D. ulrichi Foerste 1909
Orthis anticostiensis Shaler 1887

EUROPEAN SPECIES OF *PLÆSIOMYS*

- Orthis (Dinorthis) flabellulum carrickensis* Reed 1917
O. inflata Salter
O. porcata McCoy 1846
O. solaris von Buch
O. (D.) striato-costata Salter 1865
O. (D.) subdivisa Salter 1865

AMERICAN SPECIES OF *RETRORSIROSTRA*

- Dinorthis carleyi* (Hall) 1860
D. carleyi insolens Foerste 1909
D. retrorsa (Salter) 1858

ANTICOSTI SPECIES OF *PIONORTHIS*

- Dinorthis carletona* Twenhofel 1928
Orthis sola Billings 1866

DISTINGUISHING CHARACTERS.—*Dinorthis* is characterized chiefly by its convexo-concave profile, subquadrate and anteriorly bilobate plan of the ventral muscle field, *Orthis*-type brachioophores, crenulated myophore, and pallial sinuses. From *Orthis s. s.* it differs in its contour, musculature, and pallial markings.

DISCUSSION.—*Dinorthis* of the *Dinorthidæ* and *Dolerorthis* of the *Orthidæ* form an interesting homœomorphic pair, but the two can be distinguished readily by their internal features. The ventral musculature of *Dolerorthis* is like that of *Orthis s. s.* and never has the adjustor scars developed to any marked degree. The most important difference, however, is to be seen in the pallial and ovarian impressions of the two genera (see pl. 5, fig. 20, and compare with pl. 10, fig. 24). The pallial marks of *Dolerorthis* are of the *Orthis* type, two subparallel trunks given off from the anterior ends of the diductor tracks and extending directly anteriorly. They are separated by a narrow septal ridge and bound ovarian impressions which occupy nearly the entire surface of the interior lateral spaces. In *Dinorthis*, on the other hand, the ventral pallial trunks are divergent and the ovarian impressions are greatly reduced.

There is so much variation in the external contour and profile of *Dinorthis* that several distinct subgenera may be separated as follows:

1. *D. pectinella*—*Dinorthis s. s.*
2. *D. subquadrata*—*Plæsiomys*
3. *D. carleyi*—*Retrorsirostra*
4. *D. sola*—*Pionorthis*

(1) *Dinorthis pectinella* (pl. 9, figs. 2, 5) is the type of the genus and as well of the subgenus *Dinorthis s. s.* Its costate exterior differentiates it from the multicostellate exterior of *Plæsiomys*.

(2) *D. subquadrata* (pl. 9, figs. 3, 20; t. fig. 5) typifies the subgenus that was designated *Plæsiomys* by Hall and Clarke, and embraces the many species listed above.

(3) The *D. carleyi* subgenus (pl. 9, figs. 21-23), now termed *Retrorsirostra*, is characterized by its strongly procline ventral palintrope and deeply concave

ventral valve. In the ventral valve the muscle field is square in front and commonly elevated on a thickening of adventitious shell. The tribe is common in the Upper Ordovician of North America and Europe.

(4) Another subgenus of *Dinorthis* is characterized by *Orthis sola* Billings, referred by Twenhofel⁵⁵ to *Rhipidomella*; it may be called *Pionorthis* (Gr. *pion*, fat) in allusion to its biconvex profile (see pl. 9, figs. 4, 6-9, t. fig. 18). *D. carletona* Twenhofel and an unnamed species from the Upper Ordovician of the Bighorn formation belong to this subgenus.

The name *Dinorthis* was used first by Hall and Clarke, who considered its most important characters to be its reversed convexity, subquadrate muscle impressions, deltidium, and peculiar cardinal process. The same authors also proposed *Plæsiomys*, which follows the description of *Dinorthis* and is characterized by having muscle-scars like those of *Dinorthis* but an exterior similar to that of *Hebertella*. It is clear from

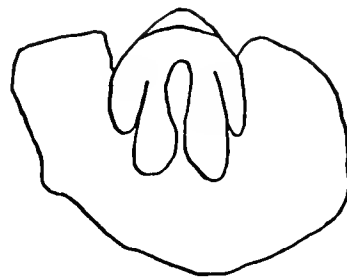


FIG. 18.—Diagram showing the ventral musculature of *Dinorthis (Pionorthis) sola* (Billings).

their descriptions that they had *O. calligramma* in mind when differentiating *Dinorthis* and were more mindful of the external resemblances of *Plæsiomys* to *Hebertella* than of the internal similarities of *Dinorthis* and *Plæsiomys*.

In the description of the interiors of *Dinorthis* and *Plæsiomys*, Hall and Clarke emphasized exactly the same features for both of their genera. This is also borne out by later studies. In an examination of a large series of these shells the present writers have been unable to find any internal generic distinction between the two. Therefore to individualize *Dinorthis* and *Plæsiomys* external characters only are available. But here, too, there is considerable difficulty in the way of a precise definition of the two genera. It was the contention of Winchell and Schuchert that there was a gradation between the external characters of *Orthis pectinella* (genotype of *Dinorthis*) and *O. subquadrata* (genotype of *Plæsiomys*). This contention they embodied in the following words:⁵⁶

⁵⁵ Mem. 154, Geol. Surv. Canada, 1927 (1928), p. 181, pl. 17, figs. 10, 11.

⁵⁶ Geol. Minn., vol. 3, pt. 1, 1895, p. 421.

From *O. pectinella* we pass to the variety *sweeneyi*, which is a local variation of it. Associated with the latter are specimens in which the strong plications begin to divide near the anterior margin. At the base of the Galena shales the strong simple, plicated forms become rarer, while those with more numerous striae prevail. Upon reaching the strata containing *Clitambonites diversa* Shaler, provisionally known to the survey as Galena shales, the numerously striated form, here described as *O. meedsi*, is the only one found. Ascending into the Galena formation for thirty or forty feet more we find *O. meedsi* still exhibiting a tendency to increase the number of its striae [costellæ], and finally assuming characters (variety *germana*) which attain their greatest development in *O. subquadrata* of the Hudson River [Richmond] formation. The change from *O. pectinella* to *O. subquadrata* is thus completed.

Consistent with this argument they placed *Plæsiomys* in the synonymy of *Dinorthis* and the same relationship was continued by Schuchert in 1897 in the Synopsis of American Fossil Brachiopoda.⁵⁷ It is, however, doubtful that such a gradation between *D. pectinella* and *Plæsiomys subquadrata* actually exists because in the Chazy (possibly Black River) of Tennessee the *Dinorthis s. s.* of that region are already showing a marked divergence toward *Plæsiomys*. The *D. transversa*, *D. quadriplicata*, and *D. interstriata* all have interstitial or dichotomous ribs. Furthermore, the *P. iphigenia* of the Black River and *P. ulrichi* of the Trenton are well established species agreeing in form and ornamentation with *O. subquadrata*.

There is still another angle at which this problem of the distinction between *Dinorthis* and *Plæsiomys* may be viewed, and that is, that *D. pectinella* and related forms represent the culmination of a trend which went in the direction of simplification of ribs. If this be true, some early *Plæsiomys* would be the ancestor of *Dinorthis*.

The value of the name *Plæsiomys* has been variously interpreted. In 1911 Raymond⁵⁸ found it "best to retain the name *Plæsiomys* for the present, and apply it to such forms as *O. subquadrata* and *O. platys* [our *Multicostella*, described farther on], in which the surface is not coarsely plicated, but is covered with striations [costellæ] which increase by bifurcation and implantation." In 1913 Schuchert⁵⁹ regarded *Dinorthis* as a subgenus of *Plæsiomys*, but later reversed the relationship.

It has been shown above that internally *Dinorthis* and *Plæsiomys* are inseparable and should be regarded as forming a single genus. But if the suggested evolutionary trend toward the simplification of ribs in *Dinorthis* be correct, it would be desirable to continue the usefulness of *Plæsiomys* by considering it as of subgeneric value. On nomenclatorial grounds *Dinorthis*

has priority over *Plæsiomys* because it appears first in Hall and Clarke's book. Accordingly we suggest that *Dinorthis* be the generic name under which the whole assemblage of these related brachiopods be designated, and to bring out the tribal relationships we propose that this genus be divided into five subgenera as defined on an earlier page.

Subgenus MARIONELLA Bancroft 1928

Pl. 8, figs. 16-18

Bancroft, Mem. and Proc. Manchester Lit. and Philos. Soc., vol. 72, 1928, p. 181, pl. 2, figs. 13-16.

GENOHOLOTYPE.—*M. typa* Bancroft 1928.

DESCRIPTION. *Exterior*.—Dinorthids of medium or small size, subelliptical in outline; hinge-line straight; cardinal extremities rounded. Lateral profile convexo-plane to convexo-concave. Anterior commissure faintly sulcate, sulcus shallow; ventral fold low, obscure. Interareas short, the ventral one apsacline, the dorsal orthocline. Ornamentation finely multicostellate.

Ventral interior.—Delthyrial cavity shallow; dental plates strong, flaring, continued as ridges about the periphery of the muscle field. Muscle area and pallial markings as in *Dinorthis*.

Dorsal interior.—Notothyrial platform shallow; brachio-phores of the *Orthis* type as developed in *Dinorthis*; cardinal process slender, simple, adductor field small.

GEOLOGIC RANGE.—The single known species, *M. typa*, comes from the Middle Ordovician of Wales.

DISTINGUISHING CHARACTERS.—*Marionella* differs from *Dinorthis s. s.* and *Plæsiomys* only in its much finer ornamentation and "the frequent, but not universal, presence of a narrow (sharply pinched up) ventral mesial fold" (p. 181).

DISCUSSION.—The genus was first placed by its nomenclator as a member of his subfamily Harknessellinae, but this reference appears to us wrong. Bancroft in a letter tells us that he now believes *Marionella* to be a subgenus of *Dinorthis*. Specimens sent by him to us are molds of the interior and exterior which give no information regarding the structure of the shell, whether punctate or impunctate. Our presumption is in favor of an impunctate test because the other internal features fit best with this type of shell, for example the simple cardinal process.

Characteristic dinorthid features occur in both valves as follows: In the ventral, the musculature and pallial markings are typical (see pl. 8, fig. 17). The cardinalia are of the orthoid type. In young forms the crenulated myophore of the cardinal process is not visible in the narrow slots of the internal molds.

Marionella is a parallel development to *Plæsiomys*, evolved probably from the British *Dinorthis*. No shells exactly like it are known in North America, and because of this independent development it deserves at least subgeneric designation.

⁵⁷ Bull. 87, U. S. Geol. Surv., pp. 215, 308.

⁵⁸ Ann. Carnegie Mus., vol. 7, no. 2, p. 239.

⁵⁹ Zittel-Eastman Text-book of Paleontology, 2d ed., vol. 1, p. 382.

Genus **VALCOUREA** Raymond 1911

Pl. 10, figs. 16, 19-23, 27-29; t. fig. 2

Raymond, Ann. Carnegie Mus., vol. 7, 1911, p. 239, pl. 35, figs. 15-19, pl. 36, fig. 1, t. fig. 12.

GENOHOLOTYPE.—*Plasiomys strophomenoides* Raymond 1905, Amer. Jour. Sci. (4), vol. 20, p. 370.

DESCRIPTION. *Exterior.*—Shells strophomenoid, hinge-line wide and straight, cardinal margins rarely submucronate or subauriculate, commonly deflected; lateral profile strongly convexo-concave, anterior commissure broadly uniplicate or faintly sulcate; dorsal sulcus shallow, in some species obsolete at the front; ventral palintrope broadly triangular, apsacline to catacline or slightly procline, delthyrium open or closed by a deltidium; dorsal interarea shorter than the ventral one, orthocline or apsacline, notothyrium partially or completely covered by a chilidium; ornamentation multicostellate, fine elevated threads in the interspaces and crossing the ribs. Test fibrous, internally impunctate; costellæ exopunctate.

Ventral interior.—Delthyrial cavity shallow, teeth strong, with accessory sockets (see t. fig. 2); crural fossettes oblique, deep; dental supports strong in young shells, obsolete in adults; cavities deep in juvenile individuals. Muscle area subpentagonal, wider and moderately bilobed in front; diductor tracks oblique, elongate, expanded in front; adductor tracks small, thin, elongate; adductor scars elongate, semielliptical; adductor track linear, enclosed by the diductor scars in front; adjustor scars prominent, situated at the base of the dental plates, as in *Dinorthis*. A small septum may be located at the base of the pedicle callist, or of the deposit under the deltidium. When a deltidium is absent a well marked pedicle callist is present. Pallial markings similar to those of *Dinorthis*, umbo-lateral spaces marked by radiating elevated ridges indicating the position of the ovarian bodies.

Dorsal interior.—Notothyrial cavity shallow; cardinalia confined to about the anterior one-fifth of the length of the valve, brachiophores forming the margin of the notothyrium, short, supported by a shell thickening beneath; sockets shallow, bounded by the sloping face of the brachiophore and an accessory tooth on the hinge margin. Cardinal process large, having a prominent shaft, and a crenulated myophore as in *Dinorthis*; chilidium present; median ridge short, extending as a rule approximately one-third the length of the shell.

GEOLOGIC RANGE.—Middle Ordovician (Stones River to Black River), chiefly of North America.

AMERICAN SPECIES

- Dinorthis deflecta* (Conrad) 1843
- D. loricula* (Hall and Clarke) 1892
- D. recta* (Conrad) 1843
- D. (Valcourea) strophomenoides* (Raymond) 1905
- Strophomena ventrocarinata* Butts 1926
- Valcourea magna*, n. sp.

EUROPEAN SPECIES

? *Orthis grandis* (Portlock)

DISCUSSION.—The name *Valcourea* was proposed by Raymond for "impunctate orthids with reversed valves, strophomenoid habit, well developed deltidium, simple cardinal process, and finely striated [costellate] surface." It was differentiated from *Plasiomys* by its finer ornamentation and the presence of a deltidium throughout life. These orthids form a very remarkable convergence toward the genus *Strophomena*. They may be distinguished therefrom, however, by several important features: Externally they may be distinguished by the resupinate form of *Strophomena* and the lack of this feature in *Valcourea*. It is true that the relative convexity of the valves in the latter is reversed, that is, the dorsal valve has the greater convexity. However this may be, the umbo of the dorsal valve of *Valcourea* is always convex and there is a distinct beak. In *Strophomena*, on the other hand, there is scarcely any dorsal beak and the umbo is decidedly concave. It is the change in convexity from concave at the umbo to convex in the middle and front of the dorsal valve that distinguishes *Strophomena*. The external convergence of *Valcourea* toward *Strophomena* is not carried to such a degree that the shell is resupinate, although its convexity is reversed. In the ventral valve the subquadrate plan of the muscle field of *Valcourea* readily separates the two genera. The forked cardinal process of *Strophomena* is a feature unknown in any orthid. Another difference is to be seen in the deltidia, that of *Strophomena* being apically perforate and that of *Valcourea* lacking a foramen.

Internally, *Valcourea* and *Dinorthis* (*Plasiomys*) are very similar, differing only in minor details of the pallial markings and ventral musculature. In the latter the diductor scars, although distinctly lobate in front, are not so strongly lobate as those of *Valcourea*, and the adjustors are much less divergent. The most notable difference, however, occurs in connection with the adductor impressions. Between the diductors of *Valcourea* is a double ridge which extends to the apex of the reëntrant between the diductor lobes. Upon this double ridge are situated the adductor scars which together form an elongate suboval or lanceolate impression, widest toward the front. The adductor scars of *Valcourea* are situated at the front of the muscle field; this contrasts with the same impressions in *Plasiomys*, which are located in the middle or at the back end of the field. The pallial impressions of *Valcourea* are much like those of *Plasiomys*, but differ in being less distinctly impressed and less broken up into subsidiary rami along the front margins. Furthermore, the ovarian radial ridges are larger and more distinctly marked in *Valcourea*.

Valcourea appears to be best represented in the lower Middle Ordovician of North America where the genus first appears in the Stones River group and is last seen in the Black River. The range is short but the species are widely spread during this time. In Europe one species, *Orthis grandis* Portlock, seems to belong in this association. *Valcourea* is contemporaneous with *Dinorthis s. s.* and *Pläsiomys*, but dies out long before either of these tribes.

***Valcourea magna*, n. sp.**

Pl. 10, figs. 16, 20, 27-29

Shell large, wider than long, convexo-concave to convexo-plane; dorsal valve having a faint sulcus which is lost toward the front of the shell. Ventral interarea long, strongly apsacline. Delthyrium open. Surface multicostellate, costellæ crossed by fine elevated concentric lines. Ventral muscle field bilobed in front, pentagonal in outline. Pallial marks as in *Dinorthis*.

This species is the largest of all the *Valcoureas* and, so far as known, does not have a deltidium. The concavity of the dorsal valve is less than is usual in other species.

Measurements of the holotype, Cat. No. 779, Schuchert Collection, Yale University:

| Width | Length | Thickness |
|--------|--------|-----------|
| 47 mm. | 37 mm. | 17 mm. |

HORIZON AND LOCALITY.—Ordovician (Simpson), Criner Hills, Oklahoma.

Genus MULTICOSTELLA Schuchert and Cooper 1931

(Lat. *multi*, many; *costella*, small rib)

Pl. 8, figs. 19, 22, 23, 27; pl. 15, fig. 12

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 244.

GENOHOLOTYPE.—*Orthis* (?) *saffordi* Hall and Clarke 1892, Pal. N. Y., vol. 8, pt. 1, pp. 217, 340, pl. 5A, figs. 38-40.

DESCRIPTION. *Exterior*.—Shells semielliptical, anterior margin convex; lateral margins convex or straight; hinge-line wide and straight; cardinal extremities angular or obtuse; lateral profile subequally biconvex; anterior commissure rectimarginate to sulcate; fold and sulcus absent, faintly or strongly developed; interareas nearly equal in length, the ventral usually slightly longer; ventral interarea apsacline, umbo convex, delthyrium open; dorsal interarea orthocline or faintly anacline; umbo very gently convex, usually sulcate. Ornamentation multicostellate, interspaces with elevated growth-lines; test fibrous, impunctate.

Ventral interior.—Delthyrial cavity shallow; teeth small; dental plates strong, advancing; small pedicle callist in the apex; crural fossettes shallow, oblique; muscle area nearly one-third the length of the shell, about as long as wide, bilobed in front; diductor scars elongate, expanded in front; adductor tracks elongate; adjustor scars short, narrow, slightly expanded in front. Elevated, elongate oblique lines occupy the lateral spaces next the cardinal cavities.

Dorsal interior.—Notothyrial cavity shallow; sockets shallow; brachiophores stout, blunt, supported by the thickening of the notothyrial platform; cardinal process stout, myophore crenulated; median ridge low, short; adductors not deeply impressed on the shell.

GEOLOGIC RANGE.—Middle Ordovician (Chazy) of North America.

SPECIES

Dinorthis platys (Billings) 1859

Pläsiomys brevis Willard 1928

P. elongata Willard 1928

Orthis ? *saffordi* Hall and Clarke 1892

DISCUSSION.—*Multicostella* is most closely allied to *Valcourea* and *Dinorthis* but is distinguished from both by its subequally convex valves and subequal interareas. Although a faint resupination of the ventral valve can be detected frequently in *Multicostella*, this feature is never developed to the extreme degree seen in *Valcourea* and *Dinorthis*. None of the observed specimens of the genus shows any evidence of a deltidium, but there is always a well marked pedicle callist in the apex; the absence of the deltidium in itself is not thought to be a generic character but its constant absence when combined with other peculiarities of the shell is of considerable importance. The pedicle muscle callist is a small thickened wrinkled area in the apex similar to the one of *Valcourea* when the deltidium is absent. *Multicostella* also differs from *Dinorthis* in the fineness of its radial ornamentation.

Internally the variations from *Dinorthis* and *Valcourea* are not especially striking. Perhaps the most notable one is the very moderate development of the adjustor muscles, the marked size of which in the other two genera has a marked effect on the dental plates and the shape of the muscle area. When the adjustors are greatly enlarged they crowd the dental plates outward toward the hinge-line, restricting the umbonal cavities and preventing any notable forward growth of these plates. Consequently in *Valcourea* the umbonal cavities are less pronounced than in *Multicostella* and do not ordinarily stand out as sharply defined plates. Furthermore, the expansion of the adjustor scars widens the muscle area and gives it a pentagonal outline. The dorsal valves of the two genera are in essential agreement. In *Valcourea*, however, there is a tendency toward the filling up and obliteration of the

notothyrial cavity and cardinalia which was not noticed in the genus under discussion.

Multicostella is believed to represent a side branch of the *Dinorthis* stock which flourished in Chazy time.

Genus AUSTINELLA Foerste 1909

Pl. 9, figs. 12, 15-19

Foerste, Bull. Sci. Lab. Denison Univ., vol. 14, 1909, p. 224.

GENOHOLOTYPE.—*Orthis kankakensis* McChesney 1861, Desc. New Foss., p. 77; 1868, Trans. Chicago Acad. Sci., vol. 1, p. 29, pl. 9, fig. 3.

DESCRIPTION. *Exterior*.—Transversely subelliptical to subsemicircular; hinge-line straight; cardinal angles obtuse or nearly a right angle, rarely acute; lateral profile subequally biconvex, anterior commissure sulcate. Ventral palintrope broad and long, usually gently curved, apsacline; beak slightly curved; delthyrium unmodified. Dorsal palintrope shorter than the ventral, anacline, plane; notothyrium unmodified. Ornamentation multicostellate, some costellæ hollow, with concentric elevated growth-lines, strongest in the interspaces; test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth large and strong, crural fossettes shallow, oblique; dental plates thick, strong, grooved on the inside base where the adductor muscles are impressed; muscle area quadrate or with anterior margin gently convex; margins thickened and elevated; adductor track straight, expanding anteriorly, and occupying about one-fourth the total width of the muscle area; diductor scars straight and narrow; adjustor scars deeply impressed, elongate; "vascular markings [pallial sinuses] leaving the antero-lateral angles of the [muscle] scars, and branching antero-laterally" (Foerste).

Dorsal interior.—Notothyrial cavity shallow; cardinalia confined to the hinge region; brachiophores short and thick, bluntly pointed, grooved on the inner face, resembling those of *Orthis* or *Dinorthis*. Cardinal process of the *Dinorthis* type. A median ridge extends from the notothyrial platform to the middle of the valve. Adductor scars subequal, the anterior ones subtriangular in outline; both pairs are divided by a low ridge either at right angles or slightly oblique to the median ridge.

GEOLOGIC RANGE.—Upper Ordovician and essentially North American.

AMERICAN SPECIES

Orthis kankakensis McChesney 1868

Hebertella scovillei (Miller) 1882

Plectorthis whitfieldi (Winchell) 1881

EUROPEAN SPECIES

? *Orthis stracheyi* Reed 1912

DISCUSSION.—*Austinella* is characterized by its unequally biconvex profile, *Dinorthis*-like ventral muscle and pallial markings and cardinalia.

This genus was individualized first by Foerste, who brought together species that had previously been incorrectly assigned to *Plectorthis* and *Dinorthis*. The several American species placed here form a compact group but it is a difficult one to place satisfactorily in any orthid family. The affinities place the genus nearest to *Dinorthis* and *Platysomys* but there are also present *Hebertella* characteristics. The form of the valves is not suggestive of *Dinorthis* but there is no reason to suppose that a biconvex phase of that genus did not exist. The ventral musculature in its quadrate form and the prominent development of the adjustor scars are rather suggestive of *Dinorthis*. This resemblance, however, is offset by the presence of a linear adductor track expanding somewhat in its passage toward the front and not included by the diductors, a feature that is decidedly hebertelloid. Extending antero-laterally from the front ends of each diductor scar is a short pallial trunk. According to Foerste these trunks branch antero-laterally but none of the specimens in the Schuchert Collection supports this statement. The presence of a main pallial trunk extending from the anterior ends of the diductor scars is an almost universal feature of orthid shells, but it is significant that these trunks in *Austinella* are divergent like those of *Dinorthis*. They are in contrast with those in the family Orthidæ, which extend directly toward the front of the shell, being nearly subparallel to the front margin and then diverging abruptly laterally. On the other hand, pallial trunks are rarely seen in *Hebertella* but when present are short and not widely divergent, probably because the ends of the diductor scars are convergent.

The cardinalia of *Austinella* suggest relationship with *Dinorthis* rather than with *Hebertella* or *Orthis*. The cardinal process has a crenulated myophore which excludes it at once from the Orthidæ. Winchell⁶⁰ notes the presence of a bilobed cardinal process in *A. whitfieldi*, but this was not confirmed by the specimens in the Schuchert Collection. It may have been an old specimen in which lobation of the cardinal process had taken place as in *Dinorthis* (*Platysomys*), see pl. 9, fig. 20. The myophore of the cardinal process is distinctly crenulated as shown by the one dorsal interior at hand. Foerste⁶¹ mentions having seen the interior of a dorsal valve in Dr. G. M. Austin's collection, the cardinal process of which bears "a narrow groove down the middle posteriorly." Such a groove is a common feature of *Dinorthis* (*Platysomys*). Excavation of the myophore into the shaft by the muscles has been seen also in *Dinorthis*, so that the cardinal

⁶⁰ Geol. Nat. Hist. Surv. Minnesota, 9th Ann. Rept., for 1880, 1881, p. 116.

⁶¹ Bull. Denison Univ., vol. 17, 1912, p. 131.

process comes to resemble that of *Plectorthis*, hence this is no serious objection to placing *Austinella* near *Dinorthis*. The brachiophores appear to be of the *Dinorthis* type and are supported chiefly by adventitious shell substance.

When Foerste named the genus in 1909 he stated in the introductory sentence that "*Dinorthis scovillei* belongs to a group of species typified by *Orthis kankakensis*, McChesney and including also *Orthis whitfieldi*, N. H. Winchell." This statement implied, if it did not definitely say, that *O. kankakensis* is the genotype of *Austinella*. Evidently Bassler so interpreted Foerste's words, because *O. kankakensis* is designated as the type in the Ordovician-Silurian Index, p. 1002.⁶² Later, however, Foerste⁶³ stated that "*Austinella scovillei* is regarded as the genotype of the proposed group, *Austinella*." As we have already noted, Foerste selected the genotype in 1909 and this selection must stand.

Genus PALÆOSTROPHOMENA Hortedahl 1916

Hortedahl, Videns. Skrift., I. Mat.-Naturv. Klasse, 1915, no. 12, 1916, p. 43, pl. 7, figs. 1, 2.

GENOLECTOTYPE (Öpik).—*P. concava* Hortedahl 1916 (non *Strophomena concava* Schmidt; see Öpik, Acta et Comment. Univ. Tartuensis, A, vol. 17, pt. 1, 1930, p. 57).

ORIGINAL DESCRIPTION.—General form as in *Strophomena* and *Strophonella* but differs distinctly in interior characters of dorsal valve, the cardinal process being not bilobed but as in the Orthidæ simple, having the shape of a short vertical plate, posteriorly united with the crural plates, which end rather abruptly. The cardinal process is supported by a faint median elevation in the valve stretching for some distance anteriorly. Interior of ventral valve not known.

GEOLOGIC RANGE.—Lower Ordovician (Stage 3) of Norway. The only species is the genotype.

DISCUSSION.—According to Hortedahl, this genus has a dorsal interior which clearly relates it to the orthids, but the exterior is exactly like that of *Strophomena*. This combination of characters is suggestive of *Valcourea* but according to the figures the specimens are more finely ornamented than in the latter. Furthermore, *Palæostrophomena* is provided with concentric wrinkles which are unknown in *Valcourea*. Although the exterior is very close to that of *Strophomena* it would seem best to consider this shell as an orthoid homœomorph of that genus. The simple cardinal process is unknown in the *Strophomenacea* (except in the *Plectambonitidæ*, which may be aberrant orthids),

so that it seems more reasonable to consider *Palæostrophomena* an orthid and to place it tentatively near *Valcourea*.

Öpik (1930) says that Hortedahl did not have before him specimens of Schmidt's *Strophomena concava*, but a Norwegian shell that he identified with that species. Accordingly Schmidt's form is not the genotype, as stated by Schuchert and Levene (1929), but Hortedahl's *Palæostrophomena concava* becomes the type.

Genus PLANIDORSA Schuchert and Cooper 1931

(Lat. *planus*, flat; *dorsum*, back)

Pl. 16, figs. 22, 24, 25, 27; t. fig. 19

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 244.

GENOHOLOTYPE.—*P. bella* Schuchert and Cooper 1931.

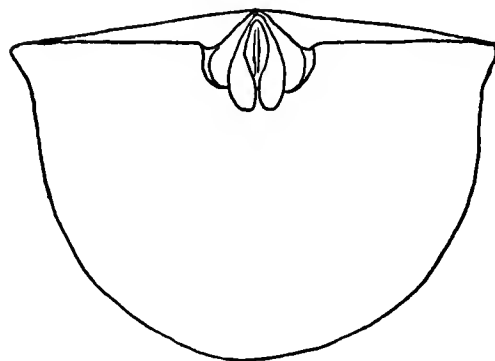


FIG. 19.—Diagrams showing the chilidial plates and ventral musculature of *Planidorsa*.

DESCRIPTION. *Exterior*.—Shells rafinesquinoid, lateral margins concave; hinge-line wide; cardinal angles acute; lateral profile plano- to slightly concavoconvex; lateral commissure straight; anterior commissure rectimarginate; fold and sulcus faintly developed in young shells; cardinal extremities set off by oblique sulci; ventral interarea longer than the dorsal, curved, slightly apsacline, beak strongly incurved, delthyrium open, umbo swollen; dorsal interarea plane, strongly anacline, notothyrium partially covered by chilidial plates and partially closed by the cardinal process also, beak undefined; ornamentation multi-

⁶² U. S. Nat. Mus., Bull. 92, 1915.

⁶³ Bull. Denison Univ., vol. 17, 1912, p. 130.

costellate, filæ over the whole surface. Test fibrous, impunctate.

Ventral interior.—Notothyrial cavity shallow; teeth small; dental plates small, nearly obsolete; muscle area rhomboidal in outline; wider than long; diductor scars elongate, tear-shaped, expanded slightly in front, not enclosing the adductors; adductor scar oval, slightly elevated, small; adjustor scars extremely large, occupying the bulk of the muscle-scar.

Dorsal interior.—Notothyrial cavity very shallow; cardinalia confined; brachio-phores short; cardinal process large, keeled on its posterior face, crenulated as in *Platymys*, protruding above the level of the dorsal interarea; median ridge long.

GEOLOGIC RANGE.—Middle Ordovician (Chazy) of North America. The only known species are *P. bella* Schuchert and Cooper and *P. crassicostella*, n. sp.

DISCUSSION.—This genus is characterized by several features that make it unique. The rafinesquinoid outline and the fineness of the ornamentation are not characteristic of any other group except *Multicostella*, and from this genus *Planidorsa* differs in its lateral profile and in the musculature of the ventral valve. There is no likelihood of confusion of this genus with *Valcourea*, which differs from it not only by its extreme change of convexity, but also in certain internal characters. The ventral musculature of *Planidorsa* is unique for the great expansion of the adjustors, and the small diductors. Another feature of interest is the presence of chilidial plates in the dorsal valve, which are uncommon among dinorthids.

Planidorsa is clearly a dinorthid, as seen in the ventral musculature and the structure of the dorsal valve. It is, however, a dinorthid having the external form of *Rafinesquina*. It is to be expected that the members of the Dinorthidæ will show the same modifications of profile as displayed by the Orthidæ and Clitambonitidæ.

Planidorsa bella Schuchert and Cooper 1931

Pl. 16, figs. 24, 25

Shell rafinesquinoid in outline and profile; ventral valve moderately convex, dorsal valve flat or slightly concave, dorsal valve with a gentle broad sulcus which is lost toward the front. Ventral interarea low, curved, apsacline. Delthyrium open. Hinge-line forming widest part of valve, subalate. In the ventral valve the dental plates are short, the adjustor scars wide, and the diductor impressions elongate. Surface multicostellate, costellæ crossed by fine elevated growth-lines, about 5 costellæ in 5 mm. at the front of the shell.

MEASUREMENTS OF HOLOTYPE (Cat. No. 764, Schuchert Collection, Yale University): Length, 17.5 mm.; width, 25 mm.

HORIZON AND LOCALITY.—Ordovician (Chazy), Waldron, Tennessee.

Planidorsa crassicostella, n. sp.

Pl. 16, figs. 22, 27

Differs from *P. bella* in not being alate and in having coarser costellæ, about 3 in 5 mm. at the front of the shell.

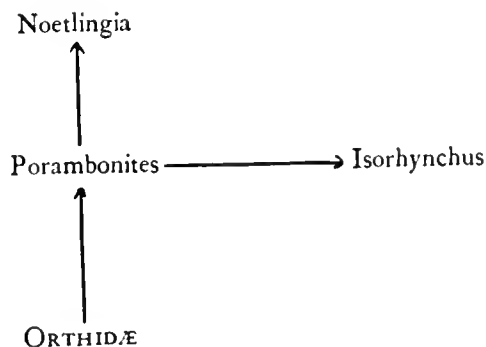
Holotype, Cat. No. 763, Schuchert Collection, Yale University.

HORIZON AND LOCALITY.—Ordovician (Chazy), Speer's Ferry, Virginia.

Family PORAMBONITIDÆ Davidson, emended

Aberrant subrostrate Orthacea derived out of Orthidæ and having a biconvex or lenticular profile, narrow hinge-line, an interarea on both valves, open delthyria, and a peculiar ornamentation consisting of flat-topped costellæ with rows of pits in the interspaces.

Table 7



Internally there are strong subparallel dental lamellæ, while the plates of the cardinalia are subparallel or divergent. In gerontic individuals these plates are frequently so covered by adventitious shell as to simulate cruralia and spondylia. There is no cardinal process in *Porambonites*, but there is a simple orthoid one in *Noetlingia*. Test fibrous, impunctate.

GEOLOGIC RANGE.—Throughout the Ordovician of northwestern Europe.

The family, although prolific in individuals and species, has but two genera, *Porambonites* Pander and its side-branch, *Noetlingia* Hall and Clarke.

The genetic relations of the family are thought to be as shown in Table 7.

Genus PORAMBONITES Pander 1830

Pl. 14, figs. 1-15, 20, 21, 24, 27-29

Pander, Beitr. Geogn. Russ. Reiches, 1830, p. 95, pl. 14, fig. 2, pl. 15, fig. 2e (*reticulata*), pl. 3, fig. 9, pl. 16A, fig. 12, pl. 28, figs. 21, 25.

Teichert, Neues Jahrb. f. Min., etc., Beil.-Bd. 63, Abt. B, 1930, pp. 177-246.

Subgenus *Isorhynchus* King, Mon. Perm. Foss., 1850, p. 112.

GENOLECTOTYPE.—Davidson in 1853 chose as the type of the genus *Terebratulites æquirostris* Schlotheim 1820, but as this is not one of the species cited by Pander in his work of 1830, it can not be so used. We shall, therefore, follow Teichert, who selects *P. reticulata* Pander.

DESCRIPTION. *Exterior.*—Subcircular to subtriangular, hinge-line narrow, producing subrostrate shells in some of the species. Cardinal extremities broadly rounded. Lateral profile nearly convexo-plane to strongly biconvex, the dorsal valve always having the greater convexity. Anterior commissure uniplicate, but the dorsal fold in many species is rather obscure, there being an elongate tongue in the ventral valve. Fold and sulcus developed only in the front half of the valves. Ventral interarea short and narrow, curved, apsacline; delthyrium open, beak commonly resorbed or abraded by the pedicle. Dorsal interarea shorter than the ventral, apsacline; notothyrium open; dorsal beak resorbed in some specimens, so that the pedicle passes through a notch in both valves. Surface ornamented by flat-topped costellæ and also by concentric elevated filæ or growth-lines which by their union in the interspaces or by alternating with each other produce the effect of pores in the radial depressions. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth strong, dental plates well developed, sharply defined in the young and early mature stages, attached directly to the floor of the valve; in a few species the anterior ends curve slightly and become convergent. In many species, in late maturity and old age the dental plates are enormously thickened, the delthyrial cavity is filled at its back end, and the dental plates are extended forward, the adventitious growth coalescing to form a structure simulating a spondylium (= spondyloid). Ventral muscle impressions lodged in the delthyrial cavity, but migrating forward as the extra testaceous matter is deposited behind. The diductor scars are semielliptical and placed partially on the inner sides of the dental lamellæ. The adductor scars occupy a linear track between the diductor impressions. The floor of the umbonal cavities in late mature or old shells is marked by prominent radial ovarian ridges.

Dorsal interior.—Notothyrial cavity deep, brachiophore short, sockets wide but shallow; brachiophore

supports prominent strong plates extended directly to the roof of the valve, always separated except when coalesced at the front by a thickening of adventitious shell. Cardinal process absent; diductor scars four in number, attached to the inner walls of the brachiophore supports. Adductor impressions in front of the anterior ends of the brachiophore supports.

GEOLOGIC RANGE.—Throughout the Ordovician of northwestern Europe. Also in the Ordovician of the Himalayas and Australia.

SPECIES

Terebratulites æquirostris Schlotheim 1820 }
Pentamerus ventricosus Kutorga 1846 }
Porambonites baueri Noetling 1883 }
P. deformatus (Eichwald) 1829 }
P. gigas Schmidt 1858 }
P. kuckersensis Bekker 1921 }
P. laticaudatus Bekker 1921 }
P. schmidtii Noetling 1883 }
P. teretior (Eichwald) 1829 }
P. wesenbergensis Teichert 1930 }
Porambonites acutiplicata Reed 1917 }
P. altus Pander 1830 }
P. bröggeri Lamansky 1905 }
P. filosa (McCoy) 1846 }
P. intercedens Pander 1830 }
P. lima Sharpe 1855 }
P. parallela Pander 1830 }
P. planus Pander 1830 }
P. reticulatus Pander 1830 }
P. ribeiro Sharpe 1855 }
P. sinuatus Reed 1915 }
P. truncata Pander 1830 }

To these species the name *Isorhynchus* may be applied in a subgeneric sense

DISTINGUISHING CHARACTERS.—*Porambonites* is recognized most easily by its peculiar ornamentation, and on the inside by the strong, divergent or subparallel brachiophore supports and dental plates.

DISCUSSION.—*Porambonites* is one of the most unique genera of brachiopods and has many interesting morphologic features. Most important among them are the external shape and ornamentation, the interareas, and the internal anatomy of both valves. The shape varies from subtriangular through subpentagonal to subquadrate and subcircular. The species are divisible into two groups on the basis of their external form. There is a group of nearly circular forms typified by *P. reticulatus* (*Porambonites s. s.*), and the other group of triangular or subpentagonal forms is typified by *P. æquirostris* or *P. deformatus*. To this latter group King's term *Isorhynchus* is applied by us. According to Teichert (chart opposite p. 226) the former characterizes BIIa-BIII divisions and the other exists from the Echinosphærites limestone to the Lyckholm of western Russia. In profile these shells are always unequally biconvex, the dorsal valve having the greater con-

vexity. In most species the fold and sulcus are usually present only below the middle of the valves. The fold is as a rule obscurely developed but in some old individuals it may be marked. The beaks are always closely appressed. In mature and old shells the beaks are generally worn away due to resorption or abrasion by the pedicle, so that a large round aperture occurs. It was Davidson's belief that the beaks had been worn away by friction in the opening and closing of the valves. The condition is not unlike that seen commonly in *Platystrophia* and other stocks with two obese valves or with the rotundity of one greater than that of the other. Continuous growth at the front margin brings the beaks into closer apposition, squeezing the pedicle, which must resorb or abrade the beaks, or have its connection with the body cavity cut off by strangulation. Beneath either beak is a short and narrow interarea. The narrowness of the interareas in such species as *P. teretior*, *P. deformatus*, *P. schmidtii*, and *P. baueri* gives them a subrostrate appearance. On the cardinal slopes, outside the interareas, is a nearly flat surface, elliptical in plan and bounded by a low groove and ridge extending from the beak. Noetling applied the name *pseudolunula* to this area, since it had been erroneously homologized with the lunule of certain pelecypods by early paleontologists. The pseudolunula is morphologically of little significance but is of use in species definition in *Porambonites*. It marks the progressive growth track of the end point of the thickening of the lateral walls of the shell.

Perhaps the most striking external feature of this genus, and the one which gave the generic name, is the peculiar surface ornamentation. This type of ornament is, however, by no means unique in *Porambonites*, being present also in *Linoporella* and *Dictyonella*. The surface is covered by fine flat-topped radial ribs which increase by bifurcation. The apparent pores arranged in radial rows in the interspaces are produced by dissepiments or cross-bars uniting the ribs. Each dissepiment alternates with its neighbor in the adjacent furrow, so that there is always a "pore" or depression opposite a cross-bar. This combination produces a fenestrated surface, resembling strongly the non-celluliferous face of a few fenestellid bryozoa. This ornamentation is a feature of the external surface only. The inner shell layer is fibrous and impunctate. In many specimens this ornamentation does not survive the rigors of life and it is completely or nearly completely worn off by solution or abrasion. This is especially true of the more delicately ornamented forms such as *P. baueri*, *P. schmidtii*, and *P. gigas*.

The features of greatest morphologic importance and interest lie within the valves of *Porambonites* and have been interpreted in various ways according to the superfamily in which one places these shells. In individuals that have the beaks externally worn or etched with acid, the internal dental plates and brach-

iophore supports show as dark subparallel or markedly divergent lines. Internally in young and mature forms these plates are sharp, discrete, and attached directly to the floor of the valve. In some species, however, *P. schmidtii* for example, the dental plates converge downward and forward quite definitely, but in their attachment to the floor of the valve they remain discrete. Late maturity and old age produce alterations in the appearance of these plates, the importance of which has been much discussed and considerably over-emphasized. In late maturity *Porambonites* spreads a callus of adventitious shell over the posterior of the shell, filling up the back portion of the delthyrial cavity and obliterating the umbonal cavities. Great thickening takes place also at the front end of the dental plates, the extra testaceous matter swelling them inward, uniting them, and forming a short anterior extension which simulates a median septum. In this way the whole structure finally assumes the appearance of a spondylium or sessile spondylium, and might be taken for such if the ontogeny were not understood. A similar development occurs in the dorsal valve. These features of *Porambonites* seen in late maturity and old age therefore can not be homologized with the spondylium simplex of *Clitambonites* and not at all with the spondylium duplex of *Pentamerus*. In the former genus there has been an actual convergence of the dental plates from the start (perhaps they were never wholly discrete) and finally they unite with a median septum. In *Pentamerus* the dental plates have grown inwardly and have united, but there is always a line of separation to show their discrete nature. *Porambonites* therefore simulates the structure of *Clitambonites* by its thick deposit of secondary shell, hiding a primitive structure that is no spondylium at all. The proper understanding of these features is thus fundamental in establishing the correct taxonomic position of the *Porambonitidæ*.

Davidson⁶⁴ proposed the family *Porambonitidæ* to embrace these shells and concluded that their position lay "between the *Rhynchonellidæ* and *Strophomenidæ*." In view of these changes Suess⁶⁵ regarded *Porambonites* as a subgenus of *Orthis*. Quenstedt⁶⁶ followed the views of Suess, placing the *Porambonites* species in his "*Orthis ventriplexæ*" along with *Platystrophia lynx* and *Orthisina anomala*. Eichwald,⁶⁷ however, erected for the genus the family *Porambonitidæ*, which he placed between the *Rhynchonellidæ* and the *Strophomenidæ* following the genus *Pentamerus*.

Noetling's paper of 1883⁶⁸ is by all means the best

⁶⁴ Brit. Foss. Brach., vol. 1, Introd., 1851-1855, p. 99.

⁶⁵ Classification der Brachiopoden, 1856, p. 112.

⁶⁶ Petrefactenkunde Deutschlands, 1870, Bd. 2, Brachiopoden, p. 541.

⁶⁷ Lethæa Rossica, Bd. 1, Abth. 2, 1860, p. 793.

⁶⁸ Zeits. deut. geol. Gesell., vol. 35, pp. 355-381.

one on this genus, and in it he attempts to show the relationship of *Pentamerus* and *Porambonites*. Indeed, he considered the relationship so close that he united the two genera in the family Porambonitidae, placing them between the Strophomenidae and the Rhynchonellidae. He thought that *Porambonites* connected the Porambonitidae to the Strophomenidae by way of *Orthosina*, and that the relationship of the former to the Rhynchonellidae was shown by the similar internal features in *Pentamerus* and *Camerophoria*. While these morphologic comparisons are correct in part, the generic relationships are now seen to be different.

Hall and Clarke⁶⁹ found the most direct relationship of *Porambonites* "in those pentameroids which have been designated as *Parastrophia* and *Anastrophia*." These affinities with the pentamerids have been continued since Noetling's time. Schuchert⁷⁰ later greatly expanded the Porambonitidae but more recently⁷¹ restricted it to *Porambonites* and *Noetlingia*.

Recently Kozlowski⁷² has also contributed information on the taxonomy of *Porambonites* and has continued the pentameroid affinities, placing the shells, however, in the order Telotremata along with the rest of the Pentameracea. This author holds that *Porambonites* has a spondylium discretum, which is rare outside of the Cambrian genus *Huenella*, in which a spondylium duplex is produced by close crowding of the dental plates. He therefore sees the origin of *Porambonites* from *Huenella*. Kozlowski places in the family, besides *Noetlingia*, *Lycophoria* also, but the abnormal orthoid cardinal process of the latter would seem argument enough to exclude this genus from the Porambonitidae.

The present writers can not subscribe to all the above, and especially do not see how *Porambonites* can be placed with the Pentameracea, for the following reasons:

(1) The universal presence in the Porambonitidae of a well defined cardinal area in both valves. This feature is only occasionally well developed in the Pentameracea (*Stricklandia*, placed here doubtfully).

(2) The presence of a prominent notothyrium.

(3) The absence of a spondylium simplex or spondylium duplex. This is the most important of the three.

It has been shown above that even in old age *Porambonites* never develops a true spondylium, since the structure usually so called is actually only a simulation of such through the addition of secondary shell. In other words, the dental and crural plates are blank-

eted by adventitious shell uniting in front. It is therefore our conclusion that *Porambonites* should be placed in the Orthacea. Verneuil⁷³ long ago suggested this relationship and Suess' classification of the brachiopods showed the same view.

The question of the actual genotype of *Porambonites* is one that needs to be adjusted, but this probably can not be done in America where extensive collections are lacking. Pander never selected a genotype, but Davidson, Hall and Clarke, and Teichert have all done so. Davidson,⁷⁴ the first to select a specific type, chose *Terebratulites æquirostris* Schlotheim, but since this species was not included in Pander's original list, it may be objected that Davidson's selection rests on insecure grounds. In defense of Davidson it may be stated, however, that he chose as genotype a form to which Verneuil had referred eight of Pander's species as synonyms, and thus in a roundabout way actually used one of Pander's species.

According to Teichert⁷⁵ it is impossible to place any of Pander's species in *T. æquirostris* Schlotheim because almost all of Pander's brachiopods were from formations below the Echinospheerites limestone, the source of Schlotheim's shell. Furthermore, this limestone is not exposed in the vicinity of Leningrad, where Pander collected most of his specimens. Therefore Pander's species belong to Teichert's first and second immigration of *Porambonites*, whereas *P. æquirostris* is of the third introduction. For these reasons Teichert believes it is impossible to use Davidson's choice of genotype.

Hall and Clarke,⁷⁶ according to the practice usual in their work, selected *P. intermedia* Pander as the genotype since it was the first species named. As Davidson's selection fails to stand according to the rules of nomenclature, that of Hall and Clarke would have to be accepted. However, this would be unfortunate, since *P. intermedia* is one of Pander's most obscure species, wretchedly figured and poorly described, and as a consequence overlooked in nearly all synonymies and catalogues.

In view of the above, it is here recommended that Pander's *P. intermedia* be thrown out as a species because it is so poorly figured and described, and because its retrieval is impossible due to the loss of Pander's types by fire. Elimination of this species will make way for the use of *P. reticulata* Pander as the genotype of *Porambonites*, as recommended by Teichert. This is a well known, excellently figured species and will make a fine genolectotype in harmony with all of the old views as to the interpretation of *Porambonites*.

⁶⁹ Pal. N. Y., vol. 8, pt. 2, 1895, p. 225.

⁷⁰ Zittel-Eastman Text-book of Paleontology, 2d ed., vol. 1, 1913, p. 393.

⁷¹ Foss. Cat., Pars 42, 1929, p. 15.

⁷² Pal. Polonica, vol. 1, 1929, pp. 127, 131.

⁷³ Geology of Russia, 1845, p. 128.

⁷⁴ Op. cit., p. 99.

⁷⁵ Private communication.

⁷⁶ Op. cit., p. 226.

Genus **NOETLINGIA** Hall and Clarke 1893

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, p. 229, figs. 159-166.

GENOHOLOTYPE.—*Spirifer tscheffkini* De Verneuil 1845, Géol. Russie, vol. 2, p. 129, pl. 2, figs. 1a-h.

DISTINGUISHING CHARACTERS.—This genus differs externally from *Porambonites* chiefly in the wider hinge-line and more distinctly developed interareas, and internally in the presence of a simple linear cardinal process.

DISCUSSION.—Hall and Clarke figure a number of “transverse serial sections” of a single specimen of the genotype which illustrate the internal structure. This is almost identical with that of *Porambonites*. In the first section the dental plates are subparallel and extend directly to the floor of the valve, and in all the other cuts these plates continue discrete except for the thickening at their bases. In the last two sections (figs. 165 and 166) the anterior ends of the plates are coalesced at their bases and produced forward as a median thickening. In the dorsal valve the brachio-phore supports have a decided curve toward each other, but the bases are always thickened and obscure. It is unfortunate that the illustrations show no distinction between the primary growth of the plates and the secondary adventitious shell. However, the sections demonstrate that *Noetlingia* is on the whole very close to *Porambonites* (see especially fig. 164), and as the geological occurrence of the two is nearly identical, it follows that *Noetlingia* is in all probability an offshoot of *Porambonites*.

Hall and Clarke (p. 229) remark that “the long, double-areaed hinge-line, the biforate umbones and suggestive external resemblance in contour to *Platystrophia*, forms a more strongly orthoid combination than has been heretofore observed among shells with such pronounced pentameroid affinities, and thus makes a more direct connection between *Porambonites* and the orthoid stock whence they have all been derived.” Under *Porambonites* we have shown that these shells belong in the Orthacea, and this conclusion is further supported by the evidence of *Noetlingia* with its orthoid cardinal process and wide interareas.

Family **LYCOPHORIIDÆ** Schuchert and Cooper 1931

Aberrant Orthacea derived out of the Orthidæ, biconvex, having strong dental plates and in the dorsal valve a simple cardinal process intimately united with the brachio-phore plates.

GEOLOGIC RANGE.—Lower Middle Ordovician of the Baltic provinces. The only genus is *Lycophoria* Lahusen.

Genus **LYCOPHORIA** Lahusen 1886

Pl. 14, figs. 16-19, 22, 23, 25, 26, 30

Lahusen, Verh. Russ. Min. Gesell., ser. 2, vol. 22, 1886, p. 221.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, p. 230, pl. 62, figs. 49-53.

GENOHOLOTYPE.—*Atrypa nucella* Dalman 1828, K. Vet. Akad. Handl. for 1827, p. 130, pl. 5, fig. 1.

DESCRIPTION. *Exterior.*—Outline globular or elongate-ovoid, hinge-line straight, narrower than the total width of the shell, cardinal extremities obtusely angular. Lateral profile strongly biconvex, the dorsal valve having the greater convexity. Anterior commissure straight or moderately uniplicate. Dorsal fold visible at the front of the valve only. Ventral inter-area very short, apsacline, delthyrium open; dorsal interarea obsolete. Beaks very small. Surface costellate; test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth large, with deep sockets; parallel to the hinge-line; extremity of tooth with a dorsad curvature; dental plates strong, extended forward as subparallel ridges nearly to the middle of the valve. In old shells the umbonal cavities are filled with adventitious deposit. The muscle field is bounded by the dental plates. The adductor scar is small, subcircular, and enclosed in front by the diductors, which are elongate and convergent in front. A low ridge separates their anterior ends in some species and is continued forward toward the front of the shell. Attachment of pedicle marked by a callus in the delthyrial cavity.

Dorsal interior.—Notothyrial cavity obsolete, brachio-phore plates and cardinal process fused, forming a trituberculate “tooth” or process which projects into the ventral valve. “Crura” are small nubs on each side of the cardinal process. On the dorsal surface of the cardinal process is a small chilidial plate similar to that seen in *Productorthis*. Muscle area quadripartite, posterior pair subtriangular or subtrapezoidal with thickened elevated lateral margin. Anterior scars forming a quarter of an ellipse in plan, divisible into two parts, an inner larger scar and a smaller outer scar.

GEOLOGIC RANGE.—Lower Middle Ordovician (Kunda formation, B₃) of Europe.

SPECIES

Atrypa nucella Dalman
Rhynchonella globosa Eichwald
R. frenum Eichwald

DISTINGUISHING CHARACTERS.—The globular form and strong biconvexity of *Lycophoria*, together with

the character of the dental plates and the peculiar fusion of the brachiophore plates with the cardinal process, are sufficient to distinguish this shell from all known brachiopod genera.

DISCUSSION.—Before proceeding to a discussion of the taxonomic position of *Lycophoria*, it will be necessary to summarize certain of its characters. The dental plates are subparallel or slightly divergent, but never do they unite medially, or even remotely resemble a spondylium, although Kozłowski thinks the muscle pit with its high margins resembles his spondylium discretum, a feature more common in occurrence than he supposed. Furthermore, one does not see in these shells any great thickening of the dental plates as occurs commonly in *Porambonites*. The mantle of *Lycophoria* filled up the umbonal cavities and also placed a considerable deposit of adventitious material at the back end of the delthyrial cavity, causing the muscles to migrate forward, but there is no extensive thickening of the plates themselves. Judged from the ventral valve, alone, one might be inclined to place these shells with *Porambonites*, as Kozłowski has done, but the dorsal valve shows departures too radical to justify this reference.

In the dorsal valve, the cardinalia and the muscle impressions are the chief structures of interest. The "cardinal process," so called, consists of four distinct parts: (1) the chilidium, (2) the cardinal process proper, (3) the brachiophores, and (4) the "crura."

(1) The chilidium is a thick, subcircular plate lying over the base of the cardinal process, bent ventrally on both sides and also dorsally at the front end. It reminds one much of the chilidium of *Productorthis* (see pl. 4, fig. 16).

(2) The cardinal process is more difficult to individualize. At its front end it is crescentic or lunate in outline, and extends under the ventral beak. In some specimens its ventral surface bears a rather deep groove. However, the process is clearly single, never being bifid at its front end as in *Derbyia*, *Triplexia*, or *Meekella*. In other words, the cardinal process, although much modified, is essentially orthoid.

(3) The brachiophores show as obscure plates convergent toward the roof of the valve and possibly uniting at their bases. These have been crowded together and have fused with the cardinal process at their posterior extremities (see pl. 14, fig. 30). The sockets are deep and excavated into the shell substance, and bear a small tooth on the outer wall above the excavation noted before. The curved posterior extremity of the tooth fits into the excavation and the small tooth articulates with the deep socket on the posterior face of the ventral tooth.

(4) The crura are long processes extending from the brachiophores on each side of the cardinal process.

They have a slight hollow groove toward their dorsal ends and appear as folded plates.

The taxonomic position of *Lycophoria* is difficult to express. Lahusen would place it with the Strophomenidæ, but in current classification it has been allied doubtfully with the Parastrophininæ. Kozłowski⁷⁷ would place it with *Porambonites* in the Porambonitidæ. Strophomenoid affinities are said to occur chiefly in the cardinal process, which, according to Hall and Clarke's⁷⁸ section is described as strongly bifid. However, the writers have been unable to find a bifid cardinal process. If Hall and Clarke's section were cut obliquely across the beaks so as to bevel the cardinal process transversely or obliquely, the tapering of the antero-ventral ends of the ventral groove would give the appearance of a bifid process. None of Lahusen's figures, nor any of the excellent interiors in the Schuchert Collection, give any indication of a bifid cardinal process. Hall and Clarke thought that the cardinal structure allied this genus to the orthoids but that "*Atrypa nucella* adds to these orthoid features the cardinal process of a streptorhynchoid, like *Triplecia* and *Mimulus*, thus presenting another point of tangency between these shells and the pentameroids."

Schuchert has persistently classified this genus, although with a query, with the pentamerids, allying it always with the Parastrophininæ. However, there is no pentamerid feature in *Lycophoria* save the biconvex valves. Kozłowski placed it in the Porambonitidæ, referring this family to the Telotremata. It has been shown—and a glance at the figures (pl. 14) will confirm this—that no characteristic pentameroid features occur in *Lycophoria*. Furthermore, we have removed the Porambonitidæ from this association and referred them to the Orthacea. The same reference, but as a separate family, is suggested for the genus now under consideration, since it shows orthoid features in the ventral interarea, open delthyrium, and discrete dental plates. In the dorsal valve it has been shown that the cardinalia have developed, by growing inwardly and fusing with the brachiophore supports, a cardinal process and chilidium. These features could be developed by the lateral crowding of such cardinalia as are seen in *Productorthis*, but we are not holding that *Lycophoria* descended from that genus.

The dorsal valve of *Lycophoria* thus forms a convergence toward the type of cardinalia so well known in *Meekella* and *Derbyia* of the Carboniferous. *Lycophoria* and *Productorthis* of the Middle Ordovician are therefore two stocks that have independently originated characters that are re-developed in other stocks (*Derbyia* and *Productus*) in the Pennsylvanian.

⁷⁷ Pal. Polonica, vol. 1, 1929, p. 131.

⁷⁸ Pal. N. Y., vol. 8, pt. 2, pl. 62, fig. 53.

Superfamily CLITAMBONACEA Schuchert 1929, emended

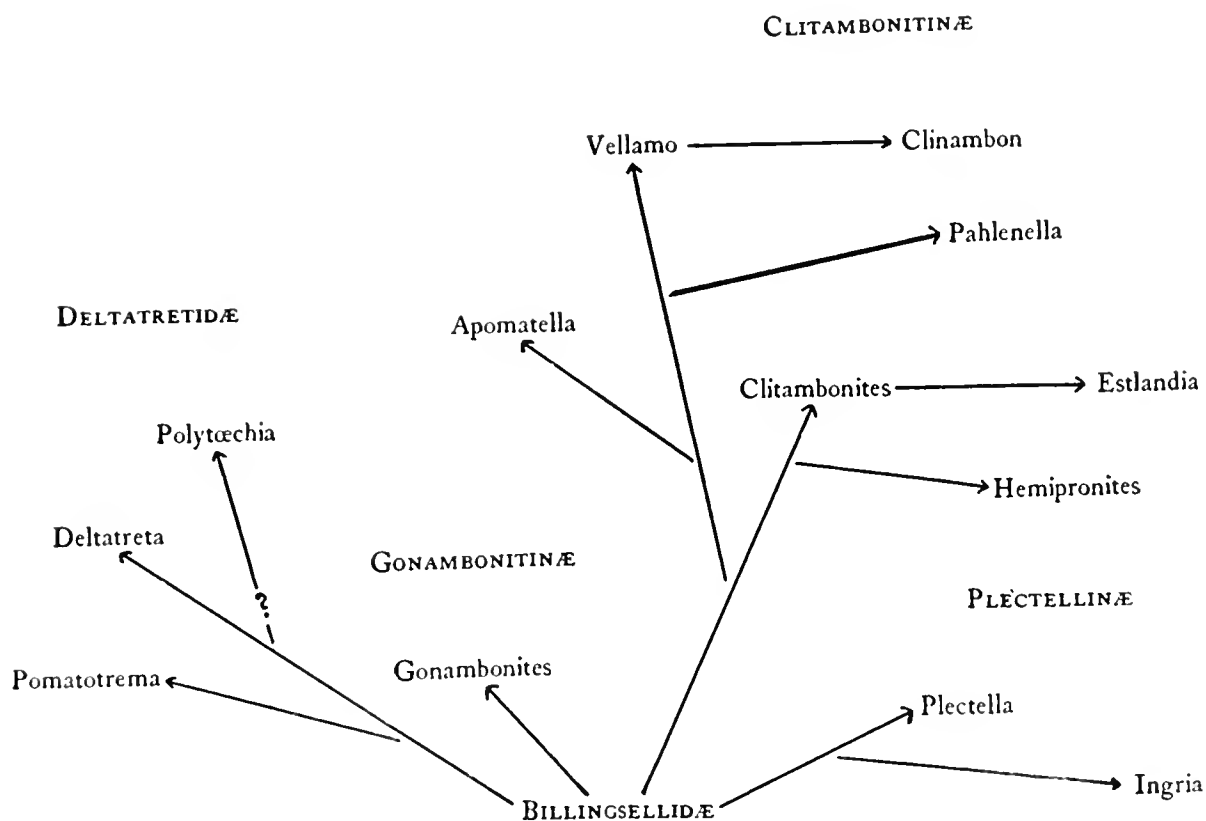
Specializing and terminal Orthoidea probably developed out of the Billingsellidæ and retaining as a rule the primitive features of deltidia and chilidia, here much enlarged, and developing either pseudospondylia (more rarely) or spondylia simplex. Test impunctate.

deltidia and cardinalia as in *Vellamo* and *Clitambonites*, but without spondylia and with discrete chilidial plates that may be remnants of chilidia.

This small family of two genera is restricted to the Lower Ordovician (upper Canadian) of the United

Table 8

Of European origin and later dispersion to North America



Range, throughout the Ordovician and rarely in the Silurian.

The phylogeny of this small superfamily is believed to be as shown in Table 8.

Family DELTATRETIDÆ Schuchert and Cooper 1931

Primitive Clitambonacea that probably originated in the Billingsellidæ. Largely orthoid in expression, with

States and Canada. It forms a morphologic connection between the orthids on the one hand and the large family Clitambonitidæ on the other. It includes the two genera *Deltatreta* Ulrich and *Pomatotrema* Ulrich and Cooper.

Internally the dorsal valves are like those of *Vellamo* and *Clitambonites*, but there are chilidial plates instead of a chilidium. In the ventral valve there is no spondylium, but in old shells of both genera there may be a pseudospondylium. The deltidium of both genera is exactly like that of the Clitambonitidæ.

Genus DELTATRETA Ulrich 1926

Pl. 6, figs. 10, 11, 13-15, 19, 30

Ulrich in Butts, Geol. Surv. Alabama, Spec. Rept. No. 14, 1926, p. 100, pl. 18, figs. 1-4 (no description and no type selected).

Syn. *Deltorthis* Ulrich, in Poulsen, Meddel. om Grönland, Bd. 70, 1927, p. 297, pl. 20, fig. 4.

GENOLECTOTYPE. — *Deltatreta fillistriata* Butts 1926.

DESCRIPTION. *Exterior*.—Resembling *Pionodema* externally, subelliptical, hinge-line straight, usually narrower than the greatest shell width; cardinal extremities obtusely subangular. Lateral profile unequally biconvex, the ventral valve usually having the greater convexity. Anterior commissure rectimarginate. Ventral palintrope long, curved, moderately or strongly apsacline; delthyrium closed by a strongly convex deltidium which is perforated near the apex by a large foramen like that of *Vellamo* and the *Clitambonitidae*. Dorsal interarea short, anacline; notothyrium partially closed by discrete chilidial plates. Surface multicostellate; shell structure fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth strong, crural fossettes prominent; dental plates strong, extending directly to the floor of the valve, defined by deep umbonal cavities. Muscle marks strongly impressed on a callus which grows under them and spreads about the inner bases of the dental plates, forming an incomplete pseudospondylium. Diductor scars elongate, situated near the base of the dental plates, not extended in front of the adductor track, the latter occupying the space between the adductor impressions and in mature and old shells continued forward as a low ridge. Lateral spaces marked by subreniform ovarian impressions as in *Orthis s. s.* and *Hemipronites*.

Dorsal interior.—Cardinalia confined to the vicinity of the hinge. Cardinal process orthoid, a linear septum. Brachiophores orthoid, supported by lateral swellings of adventitious shell exactly as in *Vellamo* and *Clitambonites*.

GEOLOGIC RANGE.—Lower Ordovician (Canadian) of the United States and Canada.

SPECIES

D. fillistriata Butts 1926

D. two n. spp. Ulrich MS.

Billingsella dice Walcott 1905

DISCUSSION.—The combination of characters in this interesting early Ordovician shell unites features seen in the later *Orthidae* and the *Clitambonitidae*. Orthoid features are the ovarian markings and discrete dental plates, clitambonitoid ones are the apically perforate deltidium and the brachiophores supported by lateral extensions of adventitious shell as in *Vellamo*.

We will first describe in detail the morphology of this genus and then discuss the peculiar nomenclatorial questions involved in the choice of a genotype. Externally *Deltatreta* has the appearance of *Pionodema* in both outline and profile and the shell is finely multicostellate with the ventral palintrope curved and apsacline as in the last named genus. The ventral interarea is marked by fine, elevated lines parallel to the posterior margins of the shell. Such elevated lines are also characteristic of *Polytaechia*. *Deltatreta* is unlike the later *Pionodema* in its possession of a perforate deltidium. Such a deltidium is unknown so far in any of the punctate shells such as *Pionodema*. The deltidium of *Deltatreta* is strongly convex, decidedly like the same feature in *Clitambonites*, and unlike that of *Billingsella* since the apical foramen is very large, and not uncommonly the foraminal margins are flexed or turned outward.

In the ventral valve the musculature and pseudospondylium are variable, depending on the age of the specimen. In young shells there is no vestige of a pseudospondylium, the adductor and diductor tracks are rather wide, and there is a prominent pedicle callist showing the inner attachment of the pedicle (see pl. 6, fig. 30). In old shells the space occupied by the adductor field is strongly elevated on adventitious shell, which is not uncommonly prolonged forward to the middle of the valve as a thick median ridge (pl. 6, figs. 13, 15). The latter may nearly completely cover the floor of the delthyrial cavity, forming a rather prominent pseudospondylium. The floor of the lateral spaces and umbonal cavities is marked by low radiating ridges, probably markings of the attachments of the ovarian bodies. In one specimen (see pl. 6, fig. 15) the ovarian impressions are subreniform as in *Orthis s. s.* or *Hesperorthis*. The palintrope and dental plates are not unlike the corresponding structures in *Hesperorthis*. The palintrope is long, and the teeth are placed considerably outside of the delthyrial margins. They are rather small but have prominent crural fossettes. The deltidium develops as in *Hesperorthis* and *Clitambonites*. It is an arch built with its sides attached to the ventral surface of the narrow flange of the palintrope which overhangs the delthyrial margins. The scar of pedicle attachment is not confined to the callist at the apex but can be traced on the sides of the dental plates and on the ventral surface of the deltidium; on the dental plates its margin runs from the antero-lateral extremity of the callist as a low ridge in an antero-dorsal direction, nearly parallel with the sloping edge of the dental plates, and then passes to the ventral surface of the deltidium some distance behind the foramen.

The dorsal valve is usually less convex than the ventral and has a shorter palintrope, and the notothyrial cavity is rather narrow and shallow. The notothyrial platform is inconspicuous and bears a simple cardinal process which is typically orthoid. The brach-

iophores are likewise orthoid and supported by adventitious shell deposited on their inner and dorsal surfaces. This adventitious material may be extended laterally for some distance (see *D. dice* (Walcott)) so that the cardinalia of *Deltatrete* resemble markedly those of *Clitambonites*. The median ridge given off from the notothyrial platform extends nearly to the middle of the valves as is usual in orthoid shells. The sockets are the cavities formed by the envelopment of the brachiophores by adventitious substance and by the sloping outer face of the brachiophore.

Deltatrete, like many orthoid brachiopods, possesses an incomplete chilidium composed of two discrete chilidial plates. These are low, extending from the margins of the notothyrium, and covering its sides; they are extensions built on the edges of the brachiophores along the delthyrial margins and strengthened by adventitious shell deposited on the inner face of the brachiophores. The specimens at hand are not favorably enough preserved to show the dorsal musculature.

This discussion of the genus *Deltatrete* has been prepared from material loaned by Dr. E. O. Ulrich and the U. S. National Museum. The specimens are all from the upper Canadian of Alabama and Oklahoma. We also include in this genus *Billingsella dice* Walcott, found in the drift near St. Albans, Vermont, which is very close to *Deltatrete*, n. sp. (see pl. 6, fig. 15) from northeast of the Wichita Mountains, Oklahoma.

Turning now to the nomenclatorial difficulties, the first use of the name *Deltatrete* was by Ulrich in a faunal list prepared by him for Purdue and Miser,⁷⁹ the name appearing as "*Deltatrete* cf. *electra* Billings" and unaccompanied by any description or figure. This citation is then clearly a *nomen nudum* and as such has no standing.⁸⁰

In 1926 Butts used *Deltatrete* as of Ulrich for shells collected in Alabama and Oklahoma. Two species were named and both were accompanied by illustrations and one of these has a short statement of Ulrich's conception of the genus. Since no type has ever been definitely designated for *Deltatrete*, we here select *D. fillistriata* Butts. This species has been chosen instead of *D. elegantula* Butts which appears first in the report (page 99, in reference to the figures on plate 18), because there is no characterization of the latter species and in addition it is clearly not typical of *Deltatrete* according to the views expressed for *D. fillistriata* and as indicated by Ulrich's specimens in Washington. In the plate legend (pl. 18, figs. 1-4 [p. 100]) for *D. fillistriata*, Butts states clearly that

⁷⁹ U. S. Geol. Surv., Geol. Folio 202, 1916, p. 5.

⁸⁰ The recent Schuchert-LeVene catalogue cites the genotype as "*D. cf. electra* Ulrich ? = *Orthis electra* Billings," with bibliographic reference to the last named species. Since, however, the name as written by Ulrich is a doubtful identification, it can not be held that he intended to place Billings' species as the type of the genus. See Rules of Nomenclature, Art. 30, II c².

Ulrich has proposed the name *Deltatrete* for shells having a deltidium. Hence *D. elegantula*, which has no deltidium, is obviously not typical of *Deltatrete* as conceived of by Ulrich. We refer it doubtfully to our new genus *Paurorthis*.

Genus POMATOTREMA Ulrich and Cooper, n. gen.

(Gr. *poma*, cover; *trema*, hole)

Pl. 16, figs. 14-16, 18-21, 23, 26, 31

GENOHOLOTYPE.—*P. muralis* Ulrich and Cooper, n. sp.

DISCUSSION.—On plate 16 the writers figure a shell that has been known as "*Orthisina*" *grandæva*, being first referred to *Orthisina* and later by Hall and Clarke to *Billingsella*. However, it does not belong to either of these, but is of a new genus which is not uncommon in the Lower Ordovician. We had provisionally referred this species to *Taffia*, but after the junior author had studied interiors of the genotype, *Taffia planoconvexa*, at Washington (unfigured by Butts) he found that the group under consideration (*Pomatotrema*) has nothing to do with *Taffia* as figured by Butts. It was Ulrich's intention to affix the name *Taffia* to shells similar to if not identical with *O. grandæva*, but in the Alabama report unfortunately *T. planoconvexa* was figured and this of course fixed the genotype of *Taffia*. Being so established, *Taffia* is not congeneric with *Orthisina grandæva*, but is a member of the family Orthidæ.

The junior author discovered the differences between *Taffia* and *Pomatotrema* after he had removed from Yale University to the U. S. National Museum, and after he had agreed to collaborate with Dr. E. O. Ulrich in a study of the Ozarkian and Canadian brachiopods. Consequently the new genus *Pomatotrema* born by the above union bears as its author the names Ulrich and Cooper, with *P. muralis* Ulrich and Cooper as the genoholotype. The following discussion of the genus is based on material in the U. S. National Museum and the figured specimens from Newfoundland in the Schuchert Collection at Yale.

DISTINGUISHING CHARACTERS.—Plano-convex in lateral profile, with perforate deltidium, chilidial plates, and subparallel or ventrally convergent dental plates.

Pomatotrema muralis Ulrich and Cooper, n. sp.

Pl. 16, figs. 15, 20

Shell small or medium-sized, nearly as wide as long, cardinal extremities nearly a right angle. Ventral interarea long; delthyrium longer than wide, covered by a prominent convex deltidium which is apically perforate as in *Pellamo*. Notothyrium partially closed by chilidial plates. Surface multicostellate, about 3 costellæ to 1 millimeter at the front of the shell. Dental

lamellæ strong, adductor field lanceolate, enclosed by the subrescentic diductor scars. Pallial trunks as in *Orthis s. s.*, bounding subreniform ovarian impressions. In the dorsal valve the brachiophores are simple rods supported by lateral growths of shell substance as in *Vellamo*. Cardinal process simple. Adductor field subflabellate, anterior scars the smaller. Inside the margin of the valve is a thick subperipheral rim.

To this genus also belong *Orthisina grandæva* Billings, and *Clitambonites semiconvexus* Poulsen.

HORIZON AND LOCALITY.—Ordovician (Canadian), SW $\frac{1}{4}$ Sec. 2, T 1 S, R 1 W, about 4 miles east of Hennepin, Oklahoma.

Genus POLYTÆCHIA Hall and Clarke 1892

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, p. 239, pl. 7a, figs. 26-30, t. figs. 11, 12.

Hom. *Ivaagenia* Hall 1889.

GENOHOLOTYPE.—*Hemipronites apicalis* Whitfield 1886, Bull. Amer. Mus. Nat. Hist., vol. 1, p. 300, pl. 24, figs. 1-5 (non *Orthis? apicalis* Billings).

ORIGINAL DESCRIPTION.—Shell small, subtriangular in contour. Hinge-line straight, about equaling the diameter of the shell. Pedicle-valve with a high, nearly vertical cardinal area marked with oblique striations parallel to the lateral margins. Delthyrium covered by a narrow, convex plate; the presence of a foramen not determined. On the interior the dental lamellæ are widely separated, and descend along the umbonal cavity for a short distance vertically, thence bending sharply inward and meeting at a low angle in the median line; thus forming, with the deltidium, a conspicuous subrostral vault. This inner spoon-shaped plate, spondylium, is supported by a stout median septum, and two smaller lateral septa, which meet it at the lines of angulation; the former of these extends for the entire length of the plate, while the latter is free from the accessory septa near its anterior edge. The umbonal cavity of the valve is thus divided into five chambers, and in the lateral chambers there is still another septum, lower than the rest and not extending to the spondylium. The brachial valve is shallow and depressed-convex, with a narrow cardinal area. The delthyrium is very broad with a partially developed covering, the dental sockets are widely separated, the crural plates narrow and nearly parallel to the hinge-line. The cardinal process is simple, linear and quite prominent, and at its union with the crural plates is a subtriangular thickening which is supported by a low median septum. Surface covered with fine, elevated, radiating striæ, without evidence of median fold and sinus.

GEOLOGIC RANGE.—Canadian (Beekmantown) and Chazy?

AMERICAN SPECIES

Hemipronites apicalis Whitfield 1886

Polytæchia symmetrica Butts 1926

P. ? oakensis Butts 1926

DISCUSSION.—The multicamerate apical ventral interior of this genus is characteristic of it, and shows a convergence toward similar structures in *Gonambonites s. s.* and *Clarkella*. The genus, however, can not be placed in the Syntrophidæ because of its external sculpture, shape of the valves, and internal features of the dorsal valve, which are evidently close to those of *Vellamo* or *Deltatretea*. The presence of a deltidium and chilidium are further features linking this genus intimately with the Clitambonitidæ or Deltatreteidæ.

Polytæchia appears to be an American genus only, and for this reason its relationships to *Clitambonites s. s.* are doubtful. The ensemble of the shell ornamentation, profile, etc., suggest *Deltatretea*, and were it not for the multicamerate apex it would definitely belong here. The position we assign the genus is tentative.

Family CLITAMBONITIDÆ Winchell and Schuchert 1893

Divergent specialized Protremata derived out of the Orthacea, having well developed deltidia and chilidia. In the ventral valve the muscles are usually borne on a spondylium simplex. In the dorsal valve the cardinalia are of the *Orthis* type, supported by lateral adventitious shell growths. Ventral, pallial, and ovarian markings essentially the same as those of *Orthis*.

DISCUSSION.—The members of the Clitambonitidæ, prolific in variable individuals, have until recently been classified in the Pentameracea, but Schuchert in 1929⁸¹ made them the basis of a new superfamily, the Clitambonacea. This he did when he saw that the stock had a genetic origin independent of the Pentameracea, as is plainly shown by their different type of spondylia. It is true that the Clitambonacea are closely related to the Orthidæ, but as they are not in the main line of brachiopod evolution, being a specializing stock, and since most of them have peculiar deltidia and as a rule strong chilidia, and more or less well developed simple spondylia, it is thought advisable to recognize these tendencies and to separate them from the Orthacea as another superfamily, Clitambonacea.

Ventral valve.—The chief points of departure from the usual orthid structure in the Clitambonitidæ are in the spondylium and deltidium. The former is a spoon-shaped plate usually resting on the floor of the valve at its posterior end but elevated on a median septum at the front end. In a few forms the septum may be absent or may be so abbreviated as to be virtually absent. The junction of the upper ends of the spondylium with the under side of the palintrope is marked by a distinct suture at which the growth-lines of the inner surface of the spondylium end abruptly. The delthyrial margin is an elongate triangular area

⁸¹ Foss. Cat., Pars 42, p. 15.

sloping slightly ventro-laterally and formed by the inside surface of the teeth as they grow forward. It is to this surface that the deltidium is attached.

The upper surface of the spondylium is marked by concentric lines which represent periods of no growth. Superimposed upon these are longitudinal lines which are taken to represent traces of muscle markings. No signs of muscle attachment occur anywhere in the valve except on the inner surface of the spondylium, making it evident therefore that the function of this structure was one of muscle anchorage. However, the individual muscle marks have not been ascertained. In one specimen were seen four divergent longitudinal ridges on the upper surface of the spondylium. The strongest two are at the bottom, with the other ones some distance on the sides.

It is deduced from the above that the adductor muscles occupied the central part of the spondylium over the median septum, and the diductors and adjustors were located laterally on the sides of the spondylium. The scar of attachment of the pedicle was probably located at the rear. In *Hemipronites* a slight callosity at the apex indicates the scar of pedicle attachment. *Deltatrete* has a prominent pedicle callist at the apex.

The septum consists of a single piece (euseptum) and is usually prolonged to the middle of the valve or beyond. To this ensemble, consisting of a spoon-shaped plate and euseptum, Kozłowski⁸² has applied the name spondylium simplex.

The deltidium of the Clitambonitidæ is always a convex plate covering the delthyrium. Its sides are buttressed against the upper surface of the ridge formed by the growth of the teeth and are strengthened further by deposits of callus on the sides of the teeth (pl. 7, fig. 14), and in some forms on the walls of the spondylium. The upper layer of shell on the interarea appears to be continuous with the outer surface of the deltidium.

The deltidium in these forms is usually perforate and far less commonly imperforate. Usually there is a large foramen located near the apex, which suggests that this opening functioned, at least during life, as the pedicle opening. However, in some genera and species the apical foramen was sealed at or before maturity, thus doing away with this structural feature (see pl. 8, fig. 8). The apical foramen is especially well developed in *Vellamo*, and here appears to have persisted throughout life, at least in the Trenton forms. Many of the specimens from Minnesota have an elevated flange or rim about the foramen and from its position at the apex it would appear that the deltidium is formed around the pedicle by the mantle.

In the ventral valve the ovarian and pallial impressions, where visible, are similar to those of *Orthis* and *Hesperorthis*. As shown in *Hemipronites*, a pallial

sinus extends from the outside extremities of the spondylium in the position of the diductor tracks, along each side of the median ridge, bending abruptly laterally at the front (see pl. 8, fig. 10). These sinuses bound subreniform ovarian areas marked by elevated wavy ridges exactly as in the Orthidæ. In some genera these markings are much less distinct but in all they strongly suggest direct affiliation with the Orthidæ.

Dorsal valve.—The pattern of the dorsal valve in most of the genera is alike. The brachiophores are flattened or rodlike divergent plates forming the margins of the notothyrium and extending laterally into the visceral cavity of the valve. In adults the notothyrial platform is greatly thickened by adventitious shell which extends laterally onto the inner surfaces of the brachiophores and around their dorsal surface. This gives the brachiophores the appearance of being laterally prolonged plates when actually they are short and hidden within the extra testaceous matter. The postero-lateral face of the brachiophore, however, always forms the inner wall of the socket, while on the outer wall a denticle can usually be seen which articulates with the socket in the postero-lateral face of the tooth.

The chilidium is formed similarly to the deltidium. It is a convexly arched plate built against the sides of the notothyrium and cemented by deposition of adventitious shell under the brachiophores and under the anterior side of the chilidium. Not infrequently adventitious deposit is laid on the ventral surface of the brachiophore and continuously with the front margin of the chilidium. The precise function of the chilidium is, at present, not known, but it may be of use to the animal in protecting the muscle attachments on the myophore of the cardinal process.

The musculature of the dorsal valve is like that seen in *Orthis*, *Hesperorthis*, and other orthids. There are four adductor scars divided centrally by a stout median ridge and horizontally by ridges at right angles to the median elevation. The median ridge, its lateral ridge, and the continuous curved ridges of the chilidium and lateral thickenings under the anterior face of the brachiophores give the appearance of an anchor when the shell is inverted with the posterior toward the observer. This analogy was emphasized by Pahlen⁸³ in his study of the genus *Orthisina*. The anterior pair of adductors are not uncommonly divisible into two separate scars, as in *Productorthis*.

The cardinal process is simple, orthoid in structure, and may be continued posteriorly so as to unite with the inner surface of the chilidium. Pallial markings are usually not clearly visible in the dorsal valve. Most shells show two oblique ridges extending antero-laterally from the adductor pits to a little beyond the anterior margins of the muscle field.

⁸² Pal. Polonica, vol. 1, 1929, p. 124.

⁸³ Mém. Acad. Imp. Sci. St. Pétersb., 7th ser., vol. 24, no. 8, 1877, p. 7.

AFFINITIES.—Kozłowski⁸⁴ has recently shown that the spondylium of the pentamerids, such as *Pentamerus* and *Conchidium*, has had a different origin from that of *Clitambonites* and *Skenidium*. The polyphyletic origin of this peculiar muscle platform is clear evidence of the separate origin of the two groups. Kozłowski has pointed out that the prominent development of the deltidium and chilidium in the Clitambonitidæ suggests a close relationship with the Strophomenacea, but the presence of an orthoid cardinal process and other features of the Orthidæ shows stronger affinities with the Orthacea. Before Kozłowski's paper appeared in this country, the writers had also come to the conclusion that the Clitambonitidæ were primitive, aberrant, and specialized orthids. We saw this relationship in the ventral pallial and ovarian markings, the simple septum-like cardinal process, the *Orthis*-like brachio-phores and adductor field. We now know that the presence or absence of a deltidium or chilidium is in itself not of such great significance as was formerly believed, since these features appear spasmodically in many of the later genera and families. However, an important feature of the clitambonitid deltidium is its prominent apical foramen. Kozłowski has looked with probable correctness to the Billingsellidæ as the ancestral stock of the Clitambonitidæ, and in this we agree, since the Billingsellidæ have all the necessary structures by which such a transition could be accomplished.

The writers also independently of Kozłowski saw the need of separating *Skenidium* and its allies from the Clitambonitidæ. *Skenidium* has no deltidium or chilidium, and in this respect is very specialized. The internal differences, and especially the nature of the cardinalia, link *Skenidium* with the Plectorthidæ rather than with the Clitambonitidæ. *Skenidioides*, probable progenitor of *Skenidium*, undoubtedly originated in *Finkelnburgia*, since the cardinalia of the latter are like those of the Plectorthidæ.

Öpik⁸⁵ also points out that the Clitambonitidæ in structure are foreign to the Pentameracea and places them close to his new family Plectambonitidæ. The latter family has, however, a closer relationship to the Orthacea than to the Strophomenacea, as is shown in the nature of the cardinal process and other internal structures, and it is not unlikely that more study will establish it as an aberrant and terminal division of the Orthacea. We consider the Clitambonitidæ as special developments, probably from the same ancestral stock, namely, the billingsellids.

The large family Clitambonitidæ is divisible into the following subfamilies:

Plectellinæ Öpik
Clitambonitinæ Schuchert and Cooper
Gonambonitinæ Schuchert and Cooper

Subfamily PLECTELLINÆ Öpik 1930

The Plectellinæ are primitive Clitambonitidæ without spondylia, which apparently gave rise to the specializing Clitambonitidæ of Europe.

In his splendid monograph on the Estonian Pro-tremata, Öpik⁸⁶ has proposed a family Plectambonitidæ which he defines as follows (in translation):

This family embraces all Strophomenacea with a simple cardinal process and strophomenoid habit, thus with concavo-convex or convexo-concave shells. All others, with a double cardinal process, form the family Strophomenidæ.

Heretofore the members of our new family have been combined with the Rafinesquininæ and were placed near the beginning of this subfamily.

Öpik divides his new family into three subfamilies, the Plectellinæ, Plectambonitinæ, and Sowerbyellinæ. We shall concern ourselves here chiefly with the Plectellinæ, which we believe are very close to the Deltatretidæ in structure. The Plectambonitinæ and Sowerbyellinæ in their simple cardinal process show relationships with orthoid brachiopods rather than with the Strophomenacea where they have persistently been classified. Here again external form appears to have been the chief guide in classification.

Within the Plectellinæ Öpik places *Plectella* Laman-sky, *Ingria* Öpik, and *Palæostrophomena* Høltedahl. He believes in the uniqueness of *Plectella* and in this he has the support of Kozłowski, who maintains this to be a good genus. Schuchert (1929)⁸⁷ unites *Plectella* with *Plectambonites* Pander, but in this the two European authors do not concur. In our study of these genera we are wholly dependent upon the literature and hence our conclusions may be in error. We regard *Palæostrophomena* as a possible member of the Dinorthidæ, close to *Valcourea*. The two remaining genera are characterized by having a chilidium and an imperforate deltidium. Fine radial lines mark the outside of the shells and there is no spondylium. In the dorsal valve of both *Plectella* and *Ingria* the cardinal process is orthoid, not plectambonitoid. In other words, it does not form a tentlike structure as in *Sowerbyella*. Furthermore, the brachio-phores are orthoid as in *Deltatreta* and are supported by lateral extensions of the notothyrial platform as in *Vellamo* and other Clitambonitinæ. It is our contention, then, that these shells are aberrant Clitambonitidæ, without spondylia. Development of the Plectambonitinæ and Sowerbyellinæ may have come from this line. In America, *Plectella* and *Ingria* find their nearest relatives in *Deltatreta* and *Pomatotrema*. These two genera differ from the Plectellinæ in the presence of an apical foramen and incomplete chilidium only, all other structures being in agreement.

⁸⁴ Op. cit., pp. 122-125.

⁸⁵ Acta et Comment. Univ. Tartuensis, A, vol. 17, pt. 1, 1930, p. 60.

⁸⁶ Acta et Comment. Univ. Tartuensis, A, vol. 17, pt. 1, 1930, pp. 55-58.

⁸⁷ Foss. Cat., Pars 42, p. 98.

Subfamily CLITAMBONITINÆ Schuchert and
Cooper 1931

(= Orthisininae Waagen 1884)

The typical and most prolific subfamily of the Clitambonitidæ, having a spondylium simplex. Embraces the following genera:

Clitambonites Pander
Vellamo Öpik
Clinambon, n. gen.
Estlandia Schuchert and Cooper
Hemipronites Pander
Pahlenella Schuchert and Cooper
Apomatella Schuchert and Cooper

Genus CLITAMBONITES Pander 1830

Pl. 7, figs. 17, 19-23, 26

Pander, Beitr. Geogn. Russ. Reiches, 1830, p. 70, pl. 17, fig. 6.

Syn. *Pronites* Pander, Ibid., p. 71, pl. 17, fig. 6.

Syn. *Orthisina* D'Orbigny, Compt. Rend., Acad. Sci. Paris, vol. 25, 1847, p. 267.

GENOLECTOTYPE (Dall, and Hall and Clarke).—*Pronites adscendens* Pander 1830.

DESCRIPTION. *Exterior*.—Shell semielliptical, hinge-line less than the greatest width of the valves; lateral profile biconvex or convexo-concave; dorsal valve convex; ventral valve usually subpyramidal; anterior commissure rectimarginate, dorsal valve sulcate in youth only. Ventral interarea the longer, strongly apsacline to procline; deltidium prominent, rarely perforate; dorsal interarea the shorter, usually anacline; chilidium well developed. Surface multicostellate, commonly imbricate and spinose. Costellæ crossed by elevated concentric lines of growth. Test fibrous, impunctate.

Ventral interior.—Provided with a spondylium simplex which is as wide as long or longer than wide, the sides usually flexed inward and the base usually flat. The median septum extends to about the middle of the valve. The musculature was evidently confined to the upper or inner side of the spondylium, the adductors probably at the base, the diductor and adjustor scars (if any) on the sides.

Dorsal interior.—Notothyrial cavity small, cardinal process linear, brachiophores orthoid, supported by lateral extensions of the notothyrial platform, forming, with the median septum, an inverted "anchor." Adductor field quadripartite; anterior adductor set the larger.

GEOLOGIC RANGE.—Lower and Middle Ordovician of Europe.

SPECIES (the first thirteen of Pander 1830)

*Pronites adscendens*⁸⁸
P. alta
P. convexa
P. excelsa
P. humilis
P. lata
P. oblonga
P. plana
P. præceps
P. prærupta
P. rotunda
P. tetragona
P. transversa
Orthisina schmidtii Pahlen 1877
? *Orthisina concava* Pahlen 1877

DISCUSSION.—The features best characterizing *Clitambonites* are (1) the subpyramidal ventral valve, (2) the convex dorsal valve; (3) the inclination of the ventral interarea; and (4) the external ornamentation. The ventral exterior is usually slightly convex or nearly flat, but in one exceptional species (*C. concava*) it is concave. The ventral interarea is usually catacline or decidedly procline, the angle from the horizontal being not uncommonly more than 80°, but it may also be very strongly apsacline. The dorsal valve is always more or less strongly convex, always less deep than the ventral one, with the greatest convexity usually located at the middle of the valve.

The most striking external feature of *Clitambonites*, however, is the sculpture, which sets it apart at once from *Vellamo*, the shell of the former being strongly lamellose, each interval of growth making a distinct layer ("like steps or roof-tiles," Hall and Clarke, p. 236), and the costellæ produced forward as flanges, so that there is a costellate border about the margins of the shell when they are viewed from the inside, somewhat as in *Atrypa* (see pl. 7, figs. 19, 20). This condition is approached in *Vellamo* by *V. squamata*, but in that form there are differences in the spondylium and external form that prevent its being placed in *Clitambonites*.

The deltidium of *Clitambonites* is typical of all this family, namely, wide and highly convex and perforated by a large pedicle foramen. It is interesting to note, however, that the foramen in the apex of mature shells is rarely visible, being sealed up during early maturity. It is not uncommon that the internal surface of the deltidium is strengthened by a longitudinal

⁸⁸ Verneuil (Geology of Russia) placed all of Pander's species of *Pronites* except *P. oblonga* under the name *Orthis adscendens*. From our present point of view, it seems apparent that Verneuil never understood Pander's discriminating work, and due to his great influence unjustly submerged many of the species and generic concepts of the earlier investigators.

thickening or low septum. The spondylium is sessile at its posterior extremity but is elevated on a septum in its median portion and free at the front end. The umbonal cavities commonly have some filling but never to the degree shown by *Vellamo diversa* from Anticosti.

It was Hall and Clarke⁸⁹ who revived Pander's "*Klitambonites*" as a generic term, and restricted the name, as they thought, "pretty nearly" to Pander's term *Pronites*. They, however, did not appreciate the features of *Gonambonites*, nor of the tribe of *Orthisina verneuili* which has been recently made the genotype of the genus *Vellamo* by Öpik.

Genus VELLAMO Öpik 1930

Pl. 7, figs. 5, 8-11, 14-16, 18, 24, 25, 27-32;
pl. 29, figs. 8, 14

Öpik, Acta et Comment. Univ. Tartuensis, A, vol. 17, pt. 1, 1930, p. 212.

GENOHOLOTYPE.—*Orthis verneuili* Eichwald 1841, Urwelt Russlands, II, p. 51, pl. 2, figs. 3-5.

DESCRIPTION. *Exterior*.—Shell narrowly semi-elliptical, hinge-line straight, as wide as or wider than the total width of the shell; cardinal extremities usually acutely angular. Lateral profile plano- to slightly concavo-convex; anterior commissure rectimarginate to broadly sulcate. Ventral palintrope long, strongly apsacline to catacline but never procline. Dorsal palintrope shorter, anacline. Deltidium perforate in mature forms, with the apical foramen sealed in old individuals. Surface coarsely costellate, the costellæ being crossed by fine elevated lines of growth. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep, teeth strong, forming a thickening along the sides of the delthyrial margin; crural fossettes shallow. Spondylium slightly depressed so that it is usually wider than high; median septum low but long, extending nearly to the front margin. Internal lateral spaces marked by irregular granules.

Dorsal interior.—Notothyrial cavity small, shallow, divided into two chambers by the cardinal process. Brachio-phores orthoid, supported by lateral growths anteriorly, formed by the swelling of notothyrial platform. Median ridge thick and broad, extending to the front of the muscle area; sockets shallow; adductor field quadripartite, the anterior set being the larger and divided from the posterior pair by low ridges at right angles to the median ridge. An oblique pallial ridge is given off from the antero-lateral extremities of the anterior adductor scars. Internal surface marked by low granules.

GEOLOGIC RANGE.—Middle and Upper Ordovician (Chazy to Richmond).

AMERICAN SPECIES

Orthisina diversa Shaler 1865
Clitambonites americanus Whitfield 1877
C. diversa altissima Winchell and Schuchert 1893
C. rogersensis Foerste 1910
C. ruedemanni Raymond 1921
C. trentonensis Raymond 1921
aff. *C. multicosta* (Hudson)

EUROPEAN SPECIES

Orthisina adscendens Davidson (Brit. Foss. Brach., vol. 3, pt. 7, p. 278) (non Pander).
O. complectens Wiman 1907
O. emarginata Pahlen 1877
O. pyramidalis Pahlen 1877
O. squamata Pahlen 1877
O. verneuili wesenbergensis Pahlen 1877
Orthis verneuili Eichwald 1841
Clitambonites complectens albida Reed 1917
C. humilis Fuchs
Skenidium grayia Davidson 1883
S. shallochiense Davidson 1883
Vellamo parva Öpik 1930
V. pyramidalis arcuata Öpik 1930
V. pyramidalis pahleni Öpik 1930
V. pyramidalis simplex Öpik 1930
V. ultima Öpik 1930

DISTINGUISHING CHARACTERS.—*Vellamo* is characterized externally by the wide hinge-line, apsacline palintrope, concavo- to plano-convex profile, and non-imbricate shell sculpture.

DISCUSSION.—From the above it is apparent at once that *Vellamo* differs in important details from *Clitambonites*. In the former the palintrope is usually long, flat or curved noticeably, as a rule moderately or strongly apsacline, and only very rarely catacline. *Clitambonites altissimus* and *C. trentonensis* among American species have nearly catacline palintropes. *Vellamo* differs further from *Clitambonites* in not possessing the strongly lamellose or frilled ornamentation. The surface sculpture is like that visible in the umbonal region of *Clitambonites* as pointed out by Öpik. The type of ornamentation in *Clitambonites* is approached in *Vellamo* only by *Orthisina squamata* Pahlen, which is placed here because of internal similarities.

Internally it is difficult to define any substantial difference between the two genera. The spondylium of *Vellamo* is usually wider than long and this depressed appearance is in contrast to the elongate or narrow one of *Clitambonites*. Inside the dorsal valve the fundamental structures of the two genera are essentially the same, the only perceptible variations being in a rather thicker notothyrial platform in *Vellamo* and the flange-like border around the internal margin of *Clitambonites*. Öpik points out further that the chidium of *Vellamo* is relatively short and wide and the muscle-scars generally wider and shorter, but there appears to be little generic value in these features.

⁸⁹ Pal. N. Y., vol. 8, pt. 1, 1892, p. 233.

The deltidium of *Vellamo* appears to be formed in precisely the same manner as that of *Clitambonites*, but at maturity the apical foramen is not sealed as in the latter genus though it is closed in old-age specimens.

Clitambonites appeared first geologically (Kunda), and died out with the Middle Ordovician. *Vellamo*, on the other hand, appeared later (Chazy) and endured through the rest of the Ordovician.

Genus CLINAMBON, n. gen.

(Gr. *klino*, bend, and *ambon*, umbo)

Pl. 8, figs. 24, 28

GENOHOLOTYPE.—*Anomites anomala* Schlotheim 1822, Nachträge, p. 65, pl. 14, fig. 2.

DESCRIPTION. *Exterior*.—Subquadrate in outline, valves very unequal, the ventral one pyramidal, the dorsal flat and elongate. Anterior commissure uniplacate. Ventral interarea strongly procline, longer than the dorsal one. Interarea of the dorsal valve unusually long; chilidium wide and strongly arched. Deltidium perforate in young shells but foramen sealed in old ones. Valves multicostellate as in *Vellamo*.

Ventral interior.—There is a prominent spondylium, the sides of which are infolded at the front, giving a pinched-in effect. The median septum is short.

Dorsal interior.—Exactly as in *Vellamo* except that the structures are greatly overdeveloped. The cardinal process is fused to the ventral border of the ponderous chilidium. Median ridge short. Notothyrial platform ponderous and lateral thickenings greater than in any other member of the Clitambonitidae. Brachiophores flat blades clearly visible near the sockets.

GEOLOGIC RANGE.—Middle Ordovician (Jewe and Kegel, D₂) of Estonia. The genotype is the only known species.

DISCUSSION.—The unusual development of the dorsal interarea and the ponderous chilidium are features which set this shell aside from *Vellamo*. The ornamentation is like that of the latter genus, and the appearance in the geologic column comes long after the disappearance of *Clitambonites*, indicating relationships with *Vellamo* rather than any other group of the Clitambonitinae.

Genus ESTLANDIA Schuchert and Cooper 1931

Pl. 8, figs. 6, 8, 9; t. fig. 10

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 245.

Gonambonites (pars) Öpik, Acta et Comm. Univ. Tartuensis, A, vol. 17, 1930, pp. 222-227, pl. 19, figs. 229-236, 248; pl. 20, figs. 236-239; t. figs. 24, 25.

GENOHOLOTYPE.—*Orthisina marginata* Pahlen 1877, Mém. Acad. Imp. Sci. St. Pétersb., 7th ser., vol. 24, no. 8, p. 33, fig. 8, pl. 3, figs. 11-15, pl. 4, figs. 1-3.

DESCRIPTION. *Exterior*.—Sub-strophomenoid to hebertelloid in lateral profile and outline; ventral interarea longer than dorsal, usually strongly apsacline. Deltidium having an apical foramen; chilidium complete. Surface multicostellate. Test fibrous, impunctate.

Ventral interior.—Deltthyrial cavity deep; teeth large; spondylium supported at the front by a prominent median septum and laterally by low, very short septa. Muscle attachments confined to the spondylium. Adductor and diductor tracks linear. Sub-peripheral rim low, but prominent.

Dorsal interior.—Notothyrial cavity shallow; notothyrial platform swollen, with prominent thick lateral extensions which support the brachiophores. Median ridge strong; brachiophores orthoid; cardinal process simple, cemented to the under surface of the chilidium. Subperipheral rim prominent; adductor field large, with the muscle attachments commonly elevated.

GEOLOGIC RANGE.—Middle Ordovician (Kuckers) of Europe.

SPECIES

- Orthisina marginata* Pahlen 1877
- O. pyron* Eichwald 1840
- O. volborthi* Pahlen 1877
- Gonambonites marginatus asper* Öpik 1930
- G. marginatus magnus* Öpik 1930
- G. panderi* Öpik 1930
- Hemipronites carrickensis* Reed 1917
- H. thomsoni* Reed 1917
- ? *G. inflexa* Pander 1830

DISCUSSION.—*Estlandia* differs from *Gonambonites*, which it resembles and with which it has usually been associated, in having an apical foramen, median septa in both valves, and a complete chilidium. The ornamentation of *Estlandia* and its internal structure, however, suggest relationship with *Vellamo*. As in the Orthidae, Dinorthidae, and other groups, it is reasonable to expect a convexo-concave stage of development. *Estlandia* appears, then, to be a convexo-concave stage of *Vellamo*, of rather short geological range and local development.

Genus HEMIPRONITES Pander 1830

Pl. 8, figs. 10-15

Pander, Beitr. Geogn. Russ. Reiches, 1830, pp. 71, 74, pl. 3, fig. 14, pl. 18, fig. 6, pl. 28, fig. 22.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, p. 238, figs. 9, 10.

GENOLECTOTYPE (Dall).—*H. tumida* Pander 1830.

DESCRIPTION. *Exterior.*—Shell rotund to sub-semielliptical, strongly biconvex; hinge-line straight, usually narrower than the total width of the shell; cardinal extremities obtusely angular or rounded. Anterior commissure rectimarginate; dorsal sulcus obsolete or only faintly impressed. Ventral interarea longer than the dorsal, curved, apsacline; delthyrium closed by a deltidium which is usually imperforate in adults. Dorsal interarea short, orthocline to faintly apsacline or anacline; chilidium prominent. Surface finely multicostellate; test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep, spondylium longer than wide, sessile posteriorly but supported by a low septum in front, the septum being continued forward nearly to the front margin. Adductor (?) track occupying the central depressed portion of the spondylium, diductor (?) tracks on each side at the base and partially on the sides of the dental plates. Interior lateral spaces covered by subreniform ovarian markings. Subparallel pallial impressions bounding the inner margins of the ovarian markings and separated by the median septum.

Dorsal interior.—Notothyrial cavity and sockets shallow, brachiophores orthoid, short, blunt, and supported as in *Gonambonites*. Cardinal process a linear ridge on the thick notothyrial platform. Median ridge strong, extending to the middle of the valve. Anterior adductor impressions elongate, separated from the shorter posterior pair by a narrow ridge at right angles to the median elevation. Lateral spaces occupied by pallial and ovarian markings.

GEOLOGIC RANGE.—Lower and Middle Ordovician of northwestern Europe.

EUROPEAN SPECIES (of Pander 1830 except where otherwise stated)

Hemipronites æqualis

H. alta

H. brevis

H. circularis (pl. 16, B, is same figure as *H. maxima*)

H. expansa

H. lata

H. latissima

H. maxima

H. obtusa

H. orbicularis

H. peralta

H. perlata

H. prominens

H. rotunda

H. spherica

H. transversa

H. tumida

Orthis hemipronites Von Buch 1840

O. radians Eichwald

? *H. globosa* (pl. 16, B, fig. 6). This is the same figure as *H. elongata* and both have the appearance of a *Lycophoria*

? *H. tenuistriata* Weller 1907 (China)

DISTINGUISHING CHARACTERS.—Hall and Clarke used the name *Hemipronites* for shells with tumid, subequally convex valves, hinge-line narrower than the greatest width, the greatest thickness of the ventral valve not at the beak, the surface finely multicostellate, and the deltidium non-perforate.

DISCUSSION.—*Hemipronites* differs from its nearest relative *Clitambonites s. s.* in several important characteristics. It is usually subequally convex, the ventral palintrope is never procline, and the deltidium is imperforate. This contrasts strongly with *Clitambonites* in which the ventral valve is usually subpyramidal, and the deltidium perforate at least in early maturity. The ornamentation of *Hemipronites* is also different in being much finer and in lacking the strong concentric lamellæ or frills of *Clitambonites*.

Internally there is also considerable variation between *Hemipronites* and *Clitambonites*. In the ventral valve of the former, to judge from *H. tumida*, the spondylium is sessile for most of its length but at its front end it is elevated on a low septum or ridge which extends nearly to the front margin. The walls of the spondylium are slightly convex inward and converge rapidly, forming a narrow floor at the base of the structure. This type of spondylium contrasts with that of *Clitambonites* in which it is sessile only at the posterior and is elevated on a rather high septum. The front end of the spondylium of *Clitambonites* is free and the floor rather wide.

One of the specimens in the Schuchert Collection (Cat. No. 369; see pl. 8, fig. 10) shows markings on the spondylium that can be interpreted only as the muscle impressions. Homologizing these marks with similarly situated scars in orthids, the writers believe that the central linear track represents the position of the adductor muscles. This track occupies most, but not all, of the narrow floor of the spondylium. It is bounded on each side by low ridges. The diductor impressions are thought to be narrow linear tracks located outside the ridges bounding the adductor track at the line where the dental plates unite with the septum. The impressions of these tracks are also visible for a short distance on the inside surface of the central lamellæ. They are marked off by scarcely perceptible ridges along the margin of the muscle track. Adjustor muscle impressions were not definitely determined.

Ovarian markings of irregular elevated lines are also well exhibited in the same specimen. These are subreniform areas such as are so common in *Orthis*, *Dolerorthis*, *Paurorthis*, etc. The shallow grooves separated by the median ridge and bounded by the ovarian impressions are taken to represent the two main trunks of the pallial marks, homologous to the two sinuses extending from the anterior ends of the diductors of *Orthis*, *Billingsella*, etc. It is therefore evident from the above that the important internal

shell features of *Hemipronites* differ from those of *Orthis s. s.* only in having a spondylium.

The dorsal interior of *Hemipronites* is likewise distinctly orthoid. The brachio-phores are rather flat plates, divergent and oblique to the vertical. The space between the sloping outer face of the brachio-phore and the wall of the valve forms the socket. The brachio-phores are supported and usually nearly engulfed by adventitious shell of the notothyrial platform, but never to the extent seen in *Vellamo*. The median ridge is rather high and extends to the middle of the valve. The posterior diductors are smaller than the anterior pair which are elongate and elliptical. Finally, the whole interior of the valve outside the muscle field is marked by elevated, irregular radiating ridges, and there can be no doubt that the spaces between some of these represent pallial sinuses although no definite system could be discerned.

Verneuil⁹⁰ united nineteen of Pander's species under Von Buch's name *Orthis hemipronites*. This is another example of Verneuil's "lumping" attitude and his failure to understand Pander's ability in species making. There can be no doubt that many of Pander's species of *Hemipronites* are insufficiently drawn, but even so, it must be said that all of his nineteen forms can not be put into one species. There is great need for a critical revision of the species occurring in the "Glaucinite" horizons by someone thoroughly familiar with the local stratigraphy of these shells.

Öpik has referred Pander's species *H. maximus* to the genus *Clitambonites*. A large specimen in the Schuchert Collection (Cat. No. 365), however, agrees with Pander's figure (pl. 16, B, fig. 5) except in the arching of the ventral palintrope, and it shows all the characteristics of *Hemipronites* (see pl. 8, figs. 12, 13). We believe, therefore, that Öpik has not figured *H. maxima* of Pander but actually has a new species not referable to *Hemipronites* but with a shell surface which relates it to *Vellamo squamata*.

Genus PAHLENELLA Schuchert and Cooper 1931

(After Pahlen, in recognition of his fine work on
Orthisina)

Pl. 7, figs. 1-4

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931,
p. 245.

GENOHOLOTYPE. — *Orthis trigonula (ex parte)*
Eichwald 1840, Sil. Schicht. Esthland, I, p. 148;
Pahlen, Mém. Acad. Imp. Sci. St. Pétersb., 7th ser.,
vol. 24, no. 8, 1877, p. 46, pl. 4, figs. 22-24.

DESCRIPTION. *Exterior*. — Semielliptical, hinge-
line straight; cardinal extremities acute; lateral profile
concavo-convex; anterior commissure sulcate; ven-

tral valve provided with a prominent fold. Ventral
palintrope the longer, moderately apsacline; deltidium
perforate. Dorsal interarea nearly obsolete, hyper-
cline. Surface coarsely multicostellate. Test fibrous,
impunctate.

Ventral interior. — Teeth prominent, crural fossettes
deep; spondylium short, supported by a low septum
which is not, however, produced forward beyond the
anterior end of the spondylium (see pl. 7, fig. 2).

Dorsal interior. — Notothyrial cavity nearly obsolete,
brachio-phores as in *Clitambonites* and *Gonambonites*.
Cardinal process, along with the median ridge and
notothyrial platform, fused with a sessile shield-shaped
plate of adventitious shell underneath the muscle field.
Posterior adductor scars the smaller.

GEOLOGIC RANGE. — Lower Ordovician (lower
Binn or Kunda formation) of western Russia. Only
known species the genotype.

DISCUSSION. — In this interesting little shell there are
several features that set it apart from the rest of the
Clitambonitidæ. Externally the concavo-convex pro-
file is not in itself unique, but this, when combined
with a prominent ventral fold and a corresponding
dorsal sulcus, makes an aggregate of characters suffi-
ciently distinct for generic discrimination. Internally
there are additional striking variations in each valve.
In the ventral valve, the spondylium is supported on a
septum so low as to give it the appearance of being
sessile; the septum is furthermore very short and in
this is very unlike the long ones in *Clitambonites*.

In the dorsal valve, the development of an elevated
adductor field is a convergence toward the type of
structure seen in *Leptelloidea* Jones. The disc is
shield-shaped and produced anteriorly into a short
process, while the pattern of the muscle marks does
not recall those of *Clitambonites*.

Genus APOMATELLA Schuchert and Cooper 1931

(Gr. *a*, without; *poma*, cover)

Pl. 7, figs. 6, 7, 12, 13

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931,
p. 245.

GENOHOLOTYPE. — *Orthisina ingraca* Pahlen 1877,
Mém. Acad. Imp. Sci. St. Pétersb., 7th ser., vol. 24,
no. 8, p. 48, pl. 2, figs. 18-21.

This name is suggested for the small *Orthisina*
ingraca Pahlen which is devoid of a deltidium and
chilidium. This loss of important features is a con-
vergence toward the *Orthidæ* and appeared rather
early in this genus of the *Clitambonitidæ*. The ventral
valve is subpyramidal, with a catacline or procline inter-
area. Internally the spondylium is short and elevated
upon a high septum. The interior of the dorsal valve
was not observed. The exterior is multicostellate.

⁹⁰ Geology of Russia, vol. 2, Paleontology, 1845, p. 205.

The genotype is the only known species and comes from the Canadian (Walchow) in the vicinity of Leningrad.

Subfamily GONAMBONITINÆ Schuchert and Cooper 1931

Aberrant Clitambonitidæ having a strophomenoid or substrophomenoid profile and a sessile spondylium (pseudospondylium). Dorsal and ventral median septa are lacking. In the species studied by us the deltidium is imperforate.

The subfamily embraces only the one genus, *Gonambonites* Pander.

Genus GONAMBONITES Pander 1830
sensu lato

Pl. 8, figs. 1-5, 7, 20, 21, 25, 26

Pander, Beitr. Geogn. Russ. Reiches, 1830, p. 77, pl. 3, fig. 1, pl. 16a, fig. 3, pl. 28, fig. 15.

Öpik, Acta et Comment. Univ. Tartuensis, A, vol. 17, pt. 1, 1930, pp. 220-222.

GENOLECTOTYPE (Schuchert and LeVene).—*G. lata* Pander.

DESCRIPTION. *Exterior*.—Shell strophomenoid or substrophomenoid in appearance, semielliptical; hinge-line wide and straight, cardinal extremities acutely angular; lateral profile convexo-concave; lateral commissure flexed dorsally; anterior commissure slightly sulcate, there being a faint sulcus in the dorsal valve. Ventral interarea the longer, plane, strongly apsacline; dorsal interarea short, apsacline to anacline. Deltidium imperforate in *G. planus*; notothyrium closed by a chilidium. Ornamentation multicostellate. Shell substance fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth small; spondylium (? pseudospondylium) sessile and strengthened on each side by a short lateral septum or several septa.⁹¹

The muscles were attached to the upper surface of the spondylium. The adductor tracks are linear. Diductor and adjustor scars can not be differentiated but the combined marks are situated on the sides of the dental plates. Subperipheral rim low.

⁹¹ A note in regard to the spondylium (?) of *G. planus* will be of interest. This is sessile and strongly suggests the pseudospondylium common to *Finkelnburgia* and *Linoporella*. The extra "supporting plates" are directly ventral to the dental plates and may actually be a continuation of them, and the floor of the spondylium may therefore be composed of callus. We had before us no very young shells, from which the true character of the spondylium could be ascertained. Should this ventral muscle field prove to be a pseudospondylium, the relationship of *Gonambonites planus* to the Clitambonitinae may prove to be still more remote than we had suspected.

Dorsal interior.—Notothyrial cavity shallow or obsolete; notothyrial platform swollen and extended laterally; chilidium and cardinal process protruding above the interarea. Cardinal process thin, linear; brachiophores orthoid, supported by lateral extensions of the notothyrial platform (see pl. 8, fig. 7). Sockets shallow. Adductor field subflabellate; median ridge obsolete or rudimentary. Subperipheral rim low.

GEOLOGIC RANGE.—Lower Ordovician (Canadian) of Europe (Walchow (BII) for *G. planus* Pander).

SPECIES.—We offer here no list of species because we had available for study very few forms of *Gonambonites*. Of *G. planus* there was an abundance of material, but we had no specimens of *G. latus*. We had specimens of "*G.*" *inflexus* and *G. excavatus* Pander but these do not agree morphologically with *G. planus*, from which our description was made up. We will not re-assign Pander's species from his figures or descriptions because both are rather inadequate and mistakes would be inevitable.

DISCUSSION.—The old genus *Gonambonites* has been regarded by most writers as a synonym of *Clitambonites* and was so placed by Hall and Clarke in 1892. Dall in 1877 listed *G. lata*, Pander's first species, but never selected a type. Schuchert and LeVene (1929), following Dall's lead, selected *G. lata* as the type of the genus. A little later Öpik (1930) made a critical study and revision of the genus and selected as the type *G. planus* Pander. Öpik's selection unfortunately can not stand as Schuchert and LeVene's choice has precedence.

In the description of *Gonambonites* presented above, we have based our remarks on *G. planus* for two reasons: (1) This is the only material we had available, *G. latus* being entirely lacking from the Schuchert Collection; and (2) Verneuil (Geology of Russia) placed *G. latus* in the synonymy of *G. planus*. It is a known fact that Verneuil took liberties with Pander's work that would be unheard of to-day, and it is very probable that some of the shells placed by him under *G. planus* deserve recognition as independent species. From Pander's figures of *G. latus*, there is to us a strong superficial resemblance to *G. inflexus*, a species that clearly is not a *Gonambonites*. If it is shown by subsequent workers that *G. latus* has affinities with *G. inflexus*, a wholly different interpretation of the genus will be required, and it may be found necessary to set off *G. planus* as an independent generic group on the basis of its unusual spondylium (pseudospondylium) and non-perforated deltidium.

In the absence of material, we feel obliged to follow Verneuil's interpretation of *G. latus* as a probable synonym of *G. planus*, although we feel strongly that Verneuil as a rule took many liberties. On this basis we are justified in regarding "*G. planus*" as a "cotype," as it were. Therefore, as explained under *Estlandia*, we were forced to make a new genus for shells differing very widely from *Gonambonites* as described above.

Superfamily DALMANELLACEA Schuchert and Cooper 1931

Progressive and terminal Orthoidea, probably derived out of the Orthidæ, and most easily characterized by their endopunctate test and a primitively bilobed cardinal process.

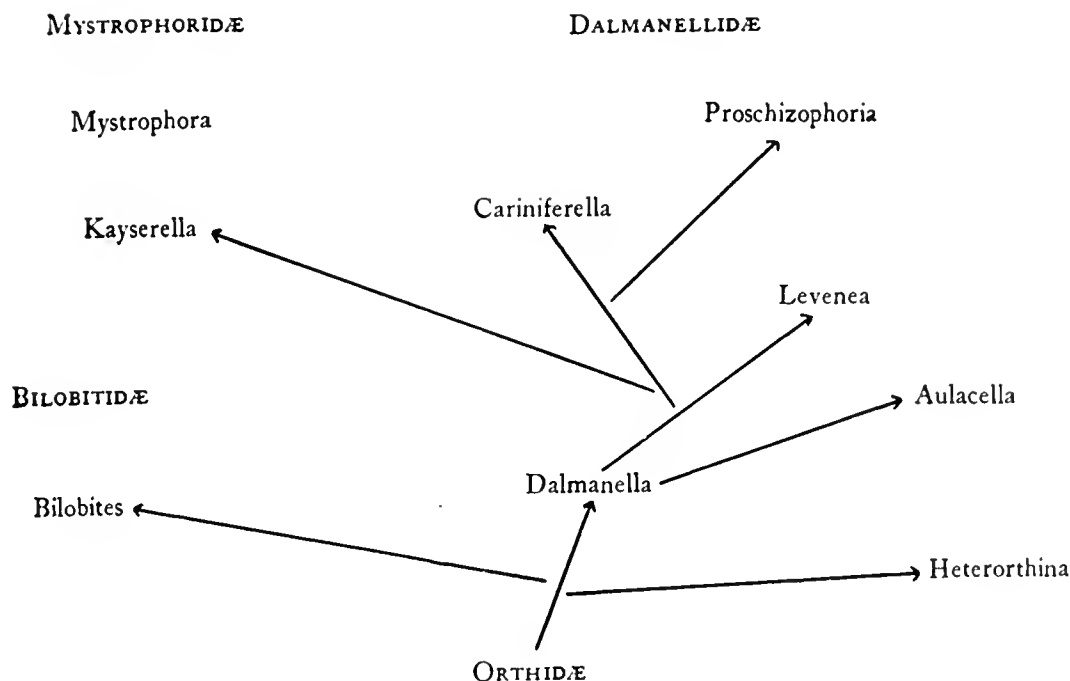
Embraces the following families:

- Dalmanellidæ Schuchert
- Wattsellidæ Schuchert and Cooper
- Bilobitidæ Schuchert and Cooper
- Mystrophoridæ Schuchert and Cooper
- Rhipidomellidæ Schuchert
- Heterorthidæ Schuchert and Cooper
- Schizophoriidæ Schuchert
- Linoporellidæ Schuchert and Cooper
- Tropidoleptidæ, n. fam.

tion. We shall not be surprised, however, if someone points out that punctation had more than one origin. Punctuation once introduced, the superfamily shows shell variations similar to those of the Orthacea, a superfamily that arose in the Cambrian, dominated the Ordovician, and vanished with the Devonian. The Dalmanellacea, on the other hand, arose early in the Middle Ordovician (first ones known in the Chazy), differentiated greatly in the late Silurian and early Devonian, spread over most of the world, constantly throwing off new genera, and yet apparently died out with the Permian.

The genetic relations seem to be as shown in Table 9.

Table 9



DISCUSSION.—As is seen in the definition of the Dalmanellacea, we lay the superfamily characteristics in the endopunctate shell and the beginning of a bilobed cardinal process. We further are forced to assume that the punctate shell started in a single species of the Orthacea, but unfortunately do not know in which of the older families this tendency originated, since in none of this superfamily is there any endopunctate species or genus. It is this utter lack of endopunctuation among the Orthacea that leads us to our assumption.

Family DALMANELLIDÆ Schuchert 1929, emended

(= Dalmanellinæ Schuchert 1913)

Progressive and terminal Dalmanellacea in which the ventral muscle field is bilobed in front, diductor scars not enclosing the adductor impressions. Brachio-phores simple, bladelike, without fulcral plates.

GEOLOGIC RANGE. — Ordovician to close of Devonian.

The family has the following genera:

Dalmanella Hall and Clarke
Cariniferella Schuchert and Cooper
Aulacella Schuchert and Cooper
Proschizophoria Maillieux
Levenea Schuchert and Cooper
Heterorthis Bancroft

Genus DALMANELLA Hall and Clarke 1892

Pl. 17, figs. 2-5, 7, 10, 13, 19-27, 29-31, 33;
 t. fig. 8

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, pp. 205, 223, pl. 5B, figs. 27-39.

Sardeson, Amer. Geol., vol. 19, 1897, pp. 91-111.

Syn. *Onniella* Bancroft.

GENOLECTOTYPE (Schuchert and Cooper).—*Orthis testudinaria* Hall and Clarke (*non* Dalman) 1892, pl. 5B, figs. 27-31 = *Orthis rogata* Sardeson 1892, Bull. Minnesota Acad. Nat. Sci., vol. 3, p. 331, pl. 5, figs. 1-4.

DESCRIPTION. *Exterior*.—Subcircular to subquadrate; hinge-line straight, narrower than the widest part of the shell; cardinal extremities rounded; lateral profile plano- to very unequally biconvex; anterior commissure sulcate, the sulcus usually being pronounced; ventral fold faint or prominent. Ventral palintrope longer than the dorsal, apsacline, beak incurved; delthyrium open. Dorsal interarea short, anacline, notothyrium closed by the cardinal process. Ornamentation fascicostellate, having prominent elevated growth-lines in the interspaces. Test fibrous, punctate.

Ventral interior.—Delthyrial cavity deep, teeth stout; crural fossettes deep; dental plates strong, flaring somewhat anteriorly; muscle field bilobed in front; diductor scars elongate, usually extending a little anterior to the front end of the adductor track; adjustor scars situated at the base of, or on the sides of, the dental plates, usually narrow, elongate. Adductor track linear, narrow or wide. Pallial sinuses consisting of a main trunk directed slightly antero-laterally, taking its origin at the anterior ends of the diductor impressions. It trifurcates shortly after its origin, one trunk being directed antero-medially, one antero-laterally, and a third secondary sinus extending directly laterally. These secondary trunks break up into subsidiary rami toward the margin.

Dorsal interior. — Notothyrial cavity completely filled by the cardinal process; brachio-phores simple, divergent, bladelike plates, subtrigonal in plan, supported only by adventitious shell deposited about the cardinal process and on the inner side of the brachio-phore. Cardinal process short, myophore trilobate or

multilobate; median ridge low, extending nearly to the front or terminating at the front margin of the muscle field. The latter small, suboval or subcircular in outline; anterior adductor scars the larger, separated from the posterior pair by low ridges at right angles to the median elevation.

GEOLOGIC RANGE.—Middle Ordovician (Chazy) to Silurian.

AMERICAN SPECIES

Orthis corpulenta Sardeson 1892

O. emacerata Hall 1860

O. futilis Sardeson 1897

O. ignota Sardeson 1897

O. meeki Miller 1875

O. multisecta Meek 1873

O. porrecta Sardeson 1897

O. rogata Sardeson 1892

Dalmanella bassleri Foerste 1909

D. resupinata Raymond 1921

D. whittakeri Raymond 1921

? *Orthis tersa* Sardeson 1892

EUROPEAN SPECIES

Dalmanella navis Öpik 1930

Onniella avelinei Bancroft 1928

O. bröggeri Bancroft 1928

O. reuschi Bancroft 1928

DISTINGUISHING CHARACTERS.—The members of this genus are to be recognized chiefly by the plano- or nearly plano-convex profile, fascicostellate exterior, bilobed ventral muscle area, and primitive brachio-phores.

DISCUSSION.—Hall and Clarke suggested the name *Dalmanella*, first using it as the "Group of *Orthis testudinaria*" under the genus *Orthis*. These authors distinguished thirteen group names under the old genus *Orthis*, but they never designated these "groups" as genera or subgenera. In describing *Dalmanella* as the "Group of *Orthis testudinaria* Dalman" they had before them American shells which they correlated with Dalman's species. The group included, however, a heterogeneous lot from which several genera have already been split. We will show that *Orthis testudinaria* Dalman *non* Hall and Clarke actually belongs to a group which is pretty much restricted to the Upper Ordovician and early Silurian and is totally distinct from the American Ordovician *Dalmanellas* with which Hall and Clarke obviously dealt in their description of the group. This situation then brings up an intricate nomenclatorial problem as to what the genotype of *Dalmanella* really is. If one adheres strictly to the rules of nomenclature, he would say that Hall and Clarke chose *O. testudinaria* of Dalman and the European species should therefore constitute the type of the genus. This would, however, restrict one of our commonest names to an heretofore obscure divi-

sion of dalmanellids, namely, *Wattsella* Bancroft, represented, among others, by two species, *D. edgewoodensis* Savage and *D. testudinaria* Dalman, both of early Silurian age. Obviously the confusion caused by so designating the genotype for a group of shells that Hall and Clarke never had in mind would be unjust to those two authors, and would offset any advantage obtained by classifying the biological properties.

Looking at the nomenclatorial problem in another way, it can be justly contended that Hall and Clarke did not have before them typical examples of Dalman's *Orthis testudinaria*, but American shells that had from the beginning been erroneously identified as this species.⁹² Therefore *O. testudinaria* of American authors in general and specifically of Hall and Clarke is not the same as *O. testudinaria* Dalman of Sweden. Accordingly, one of the several species figured by Hall and Clarke under this name can be selected as the type of the genus, and we now select as the genotype of *Dalmanella* the specimens illustrated by them on plate 5B, figures 27-31, which are of Sardeson's *Orthis rogata*.

It may be objected by "legalists" that this procedure is invalidated by Schuchert's having named *O. testudinaria* Dalman as the genotype of *Dalmanella* in his work of 1897,⁹³ a procedure in which he was followed by many others. This objection is granted willingly and would be valid if *O. testudinaria* Dalman were a native American shell, as pointed out before. Schuchert et al. never questioned Hall and Clarke's identification of the species; it was then the order of the day everywhere to identify similar shells as *O. testudinaria* Dalman throughout the Ordovician. It can be contended, further, that the followers of Hall and Clarke, by using their name unchallenged, did not alter the instability of the identification.

In further support of the contention that Hall and Clarke did not base their group discussion on *O. testudinaria* Dalman is the excellent work of Sardeson (1897) in which he describes as new species *Dalmanella*s usually referred to *O. testudinaria*. He says (p. 106):

None of the above described species are like, or similar to, Dalman's figures, and to the best of my knowledge, there is ample room for preference of Meek's view, that our forms may none of them be identical with those described as *Orthis testudinaria* by Dalman, or those identified with that species in England.

Raymond⁹⁴ corroborates this statement in the remark that "... no one seems to have proved that the real *Dalmanella testudinaria* is found in America." The present study, moreover, shows that Dalman's species actually has an internal structure totally distinct from that of *D. testudinaria* Hall and Clarke = *D. rogata* (Sardeson) and is deserving of a different generic designation.

Onniella Bancroft (pl. 17, figs. 1, 6, 8, 9, 11, 12, 18) has essentially the same internal structure as *Dalmanella* (emend.), but differs chiefly in being more transverse and having a somewhat different ornamentation. We do not consider these external details of generic value and therefore place this genus in the synonymy of *Dalmanella* (emend.). Should Paleontology progress to the point where ribbing characters are considered of value in genus making, it would probably be found that *Dalmanella meeki* will also conform to the characters of *Onniella*.

Dalmanella emacerata and *D. ignota* are among the few Paleozoic brachiopods in which nearly the full complement of muscle-scars has been observed (see pl. 17, figs. 19, 22). Sardeson figures (his pl. 5, fig. 6, of *ignota*) a specimen showing, besides the diductor, adductor, and adjustor scars, two small accessory diductor scars. The specimens that Sardeson studied are now in the Schuchert Collection and there can be little question as to the presence of these marks although they can not be seen so clearly as the figures would indicate. They are not isolated but are continuous with the diductor scars. They may actually represent the back end of the diductor impression rather than separate and special scars. The adductor marks, as in many other genera, are individually semielliptical but together form an elliptical or oval impression superimposed over the adductor track.

In the dorsal valve the brachiophores have no fulcral plates and this differentiates the true *Dalmanella* from *Wattsella* and *Idiorthis* of the Wattsellidae, at least so far as the dorsal valves are concerned. The simple, bladelike brachiophores may become spoonlike by the development of adventitious tissue on their inside surface, and then they become attached to the dorsal surface of the valve; the true brachiophore plate may in that event be almost completely obscured. A common mature and old-age condition is a growth of shell substance over the cardinal process, both shaft and myophore; and in extreme instances the adventitious shell may completely fill the notothyrial cavity and encroach on the brachiophores.

Dalmanella tersa is difficult to place, since its exterior and cardinalia are much like those of *Rhipidomella*. Furthermore, in the ventral valve the diductor scars show a marked tendency to enwrap the adductor field. The species is thus intermediate between *Rhipidomella* and *Dalmanella*, and is believed to indicate the probable origin of *Rhipidomella*.

⁹² We have learned from Doctors Reeds, Croneis, and Ruedemann, curators of the Hall material in the American Museum of Natural History, the Walker Museum of the University of Chicago, and the New York State Museum, respectively, that there are no specimens of *O. testudinaria* Dalman in these collections from Borenshult, the type locality.

⁹³ Bull. 87, U. S. Geol. Surv., 1897, p. 199.

⁹⁴ Geol. Surv. Canada, Bull. 31, 1921, p. 14.

Genus **CARINIFERELLA** Schuchert and Cooper 1931

(Lat. *carina*, keel; and *ferre*, to bear)

Pl. 18, figs. 9-12, 15, 16

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 246.

GENOHOLOTYPE. — *Orthis carinata* Hall 1843, Geol. N. Y., Rept. Fourth Dist., p. 267, fig. 1, as figured by Hall and Clarke (1892).

DESCRIPTION. *Exterior.* — Transversely semicircular, margins rounded, cardinal angles obtusely rounded; hinge-line narrower than the greatest width of the shell; lateral profile convexo-concave to unequally biconvex; anterior commissure sulcate; fold narrow, subcarinate; sulcus deep, narrow; ventral interarea short, apsacline, beak not prominent, incurved, umbo low, convex, and sulcate. Ornamentation multicostellate, with elevated growth-lines covering the whole surface. Test fibrous, punctate.

Ventral interior. — Delthyrial cavity deep; teeth strong; dental plates thick, nearly obsolete in adults; muscle field bilobed in front; diductor scars elongate, expanded anteriorly; adductor track linear, not enclosed in front by the diductor scars. Aggregate adductor scar elliptical. Adjustor scars narrow, divergent, short, placed posterior to the diductor impressions. Short pallial sinuses extending antero-laterally for a short distance in front of the diductor scars.

Dorsal interior. — Cardinalia confined to the immediate vicinity of the hinge, sockets deep, oblique; brachio-phore plates widely divergent and extending vertically to the floor of the valve, without fulcral plates; cardinal process very small, shaft short, myophore trilobed; median ridge low, extending to the anterior margin of the muscle area where it merges into the fold produced by the ventral sulcus. Muscle area small as a whole, not extending to the middle of the shell. Adductor scars separated by horizontal ridges; anterior adductors the smaller.

GEOLOGIC RANGE. — Upper Devonian.

AMERICAN SPECIES

Orthis carinata Hall 1843

Dalmanella carinata epsilon Williams 1908

D. elmira Williams 1908

D. tioga Williams 1908 (*non* Hall 1867)

D. virginia Williams 1908

D. virginia beta Williams 1908

EUROPEAN SPECIES

Cariniferella dumonti (Verneuil)

DISTINGUISHING CHARACTERS. — The distinctive features of this genus are the convexo-concave profile of the shell, the aberrant sharp fold and the corresponding deep, narrow sulcus, the *Dalmanella*-like ventral musculature, the strongly divergent brachio-phore plates, and the small muscle area of the dorsal valve.

DISCUSSION. — The members of this new genus have been referred variously to *Schizophoria* and *Dalmanella*. Schuchert referred them to the former in 1897, but in 1908 Williams⁹⁵ restudied the different species and concluded that their affinities placed them in closest association with *Dalmanella*. The combination of characters displayed by this group, however, necessitates the creation of a special designation for them.

The ventral musculature is similar to that of *Dalmanella* and *Schizophoria* in the anterior bilobation, but the adjustor scars are much shorter and more oblique, and the median ridge (euseptoid) common to the Upper Devonian *Schizophorias* is not well developed. Instead of being strongly elevated and continued in front of the diductor scars as a ridge, it is divided in *Cariniferella* and forms a distinct V in front of the diductors. Williams considers this forked septum an important character of the genus "*Dalmanella*" although it is by no means common to all the "species."

In the dorsal valve the variations of this genus from *Schizophoria* are most readily perceived in the nature of the cardinalia and the musculature. The brachio-phore plates are widely divergent, bladelike, attached directly to the inner surface of the valve. The sockets are wide and elongate and are not defined by a fulcral plate as is so characteristic in *Schizophoria*. The muscle area is rather small, but the fact that the individual scars are separated by a horizontal ridge contrasts with *Schizophoria* in which the scars are separated by an oblique ridge. In this respect *Cariniferella* resembles the genus *Proschizophoria* most closely. The adductor scars of *Schizophoria*, furthermore, are usually larger and somewhat flabellate. Pallial markings are very indistinct in most of the specimens, but when visible show the same elements common in the genus *Levenea*. There is a lateral trunk extending slightly obliquely from the ridges separating the adductors and another pair extends forward from the antero-median extremity of the anterior adductors. In *Cariniferella dumonti* the anterior trunks bifurcate near their point of origin so that there are four trunks originating in the same points as the pallial sinuses of *Levenea*. *Cariniferella* is evidently an Upper Devonian branch of the Dalmanellidæ, aberrant chiefly in its external form.

Genus **AULACELLA** Schuchert and Cooper 1931

(Gr. *aulax*, furrow)

Pl. 19, figs. 7, 8, 10, 11, 13

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 246.

GENOHOLOTYPE. — *Orthis eifelsenis* de Verneuil 1850, Bull. Soc. Géol. France, 2d ser., vol. 7, p. 25.

⁹⁵ Proc. U. S. Nat. Mus., vol. 34, pp. 38-41.

DESCRIPTION.—This genus externally resembles *Rhipidomella* and *Thiemella* but has a well marked fold on the ventral valve and a sulcus on the dorsal which are not reversed in the young stages. Internally the arrangement of the ventral muscle-scars is similar to that of *Rhipidomella* in the imprisonment of the adductor field by the diductor scars. The diductor impressions are never broadly flabellate as in *Rhipidomella* and the adjustor marks are usually clearly visible as in *Cariniferella*. Furthermore, the diductor impressions are separated by a low ridge which is forked much as in *Cariniferella*. This is a feature never shown by *Thiemella* or *Rhipidomella* in which the median ridge is always direct and unforked.

In the dorsal valve the cardinalia are ponderous and strongly resemble those of *Cariniferella* and *Rhipidomella* but are totally unlike those of *Thiemella* which are delicate and confined. In our classification *Aulacella* is placed in association with *Dalmanella* and *Cariniferella* because of the close similarity of the ventral musculature and dorsal cardinalia.

The only known species is the German *Orthis eifelensis*.

Genus PROSCHIZOPHORIA Maillieux 1911

Pl. 19, figs. 25, 26, 30, 32

Maillieux, Bull. Soc. Belge Géol., Pal., d'Hydrol., vol. 25, 1911, p. 177, pl. B, fig. 1.

GENOHOLOTYPE.—*Orthis personata* Zeiler 1857, Verh. Nat. Hist. Ver. Bonn, vol. 14, p. 48, pl. 4, figs. 9-11, emend. Kayser 1892, Jahrb. k. Preuss. Geol. Landesanst., for 1890, p. 98, pl. 11, figs. 3-5, pl. 12, figs. 1-4.

DESCRIPTION. *Exterior.*—Like *Schizophoria*, shell large and thick.

Ventral interior.—Delthyrial cavity deep; teeth large; dental plates thick and strong, continued as ridges for some distance around the margins of the diductor scars; muscle area large, cordate, wider than long; diductor scars large, divergent, not enveloping the adductor scars in front; adductor impressions forming two semielliptical impressions, together making an oval scar; the adjustor scars elongate marks on the outside of the diductor impressions.

Dorsal interior.—Cardinalia ponderous; brachio-phores as in *Cariniferella*, divergent; sockets deep; shaft of cardinal process a stout linear ridge, rounded ventrally and continued forward nearly to the anterior ends of the adductor scars; adductor impressions subequal, separated from each other by low ridges at right angles to the median ridge.

GEOLOGIC RANGE.—Lower Devonian (Coblentzian) the only known species being the European *P. personata* (Zeiler).

DISTINGUISHING CHARACTERS.—This genus differs from *Schizophoria*, which it most closely resembles, by

the cordate ventral muscle area. The ventral adductor ridge so prominent in *Schizophoria* is lacking here. In the dorsal valve the adductor scars are subequal in size and separated by a horizontal ridge at right angles to the median elevation. The prominent cardinal process without expanded myophore is another significant variation from *Schizophoria*.

DISCUSSION.—The name *Proschizophoria* was not happily chosen, as this genus is neither the earliest of the Schizophorias nor is it the progenitor of the group. The structure of the dorsal valve obviously relates it to *Cariniferella* and the Devonian representatives of the Dalmanellidæ. Neaverson⁹⁶ places *Orthis provulvaria* Maurer in this genus, but its dorsal valve has the musculature and pallial markings of *Schizophoria*.

Genus LEVENEAE Schuchert and Cooper 1931

Pl. 18, figs. 19-23, 25-32; t. fig. 14

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 246.

GENOHOLOTYPE.—*Orthis subcarinata* Hall 1857, 10th Rept. N. Y. State Cab., p. 43, figs. 1, 2.

DESCRIPTION. *Exterior.*—Subquadrate to subcircular in outline, hinge-line narrower than the greatest shell width; cardinal extremities rounded; lateral profile unequally biconvex to plano-convex; ventral inter-area longer than dorsal, apsacline; delthyrium open. Notothyrium closed by the cardinal process. Surface multicostellate. Test fibrous, punctate.

Ventral interior.—Delthyrial cavity deep; teeth strong, located at the angle of the delthyrial and hinge margins. Crural fossettes deep. Dental plates strong in the young, obsolete in old forms, thickened on the inside to form the fossette. Muscle field pentagonal in outline; diductor tracks deeply impressed, elongate; adductor track wide, elevated, shorter than the diductor marks. Adjustor tracks located on the sides of the dental plates, strongly impressed. Pallial markings as in *Isorthis* and *Schizophoria*.

Dorsal interior.—Brachio-phore plates blades like those of *Dalmanella*; cardinal process prominent, shaft short or obsolete, myophore lobate; adductor field subcircular or widely elliptical; adductor scars subequal. Pallial markings similar to those of *Isorthis* (see t. fig. 14).

GEOLOGIC RANGE.—Silurian to Middle Devonian.

AMERICAN SPECIES

Orthis lenticularis Vanuxem 1842

O. quadrans Hall 1861

O. subcarinata Hall 1857

Dalmanella macra Dunbar 1920

D. subcarinata Dunbar 1919 (*non* Hall)

? *Orthis concinna* Hall 1859

? *O. solitaria* Hall 1860

⁹⁶ Stratigraphical Palaeontology, 1928, p. 256.

EUROPEAN SPECIES

Orthis canaliculata Lindström 1860

DISTINGUISHING CHARACTERS.—*Levenca* is most like *Isorthis* in all except cardinalia, but differs in its unequally biconvex or plano-convex lateral profile, and pentagonal ventral muscle field. This genus is close to *Isorthis* in its ventral interior but differs in having less widely divergent pallial markings. In the dorsal valve it differs still more strongly from *Isorthis* in not having a fulcral plate, or as elongate an adductor field.

DISCUSSION.—Of special interest in *Levenca* is the remarkable deposition of adventitious shell, especially in the dorsal valve about the various structures of the cardinalia. Shell matter is laid on the inside surface of the brachiophores and extends around their dorsal face to the wall of the valve. The socket is a deep excavation in this adventitious shell and in some specimens may simulate a socket-plate (see pl. 18, figs. 19, 21, 29). This support of the brachiophore plates is exactly the same as that seen in *Dalmanella* s. s. The cardinal process is usually rather small and bilobed, without a pronounced shaft. In old forms a secondary shaft is produced forward over the median ridge. In such specimens the process has the appearance of a fly's head with proboscis protruded.

This genus is named for Miss Clara Mae LeVene, in recognition of her assistance in the preparation of this monograph: first, by long-continued bibliographic work on the brachiopods, begun in connection with the second edition of Zittel-Eastman in 1913, and carried on to form the basis for the Schuchert-LeVene generic catalogue of 1929; and second, by editorial revision and other work accompanying the transformation of the hand-written manuscript into the present printed volume.

Genus HETERORTHINA Bancroft 1928

Pl. 17, figs. 17, 28, 32; pl. 18, figs. 1-8

Bancroft, Mem. and Proc. Manchester Lit. and Philos. Soc., vol. 72, 1928, p. 59.

GENOHOLOTYPE.—*H. præculpta* Bancroft 1928.

DESCRIPTION.—Externally the shells of this genus resemble *Heterorthis* in outline, but the dorsal valve, instead of being flat or concave, is very gently convex and bears a shallow sulcus. The surface is rather finely multicostellate. In the ventral valve the teeth are short and flaring and their anterior ends are continued forward as low ridges along the outer margins of the diductor scars. The muscle area is long, extending nearly to the middle of the valve or a little beyond. It is strongly lobate in front, the diductor scars are elongate with subparallel sides, and their anterior ends extend in front of the elongate adductor track. Adjustor marks were not seen.

In the dorsal valve the cardinalia are similar to those of *Dalmanella*. The brachiophore plates are bladelike, divergent, supported by adventitious shell, which forms a rather thick notothyrial platform. The cardinal process is small, the shaft short, the myophore lobate. The adductor field is somewhat shield-shaped with individual scars subequal.

DISCUSSION.—*Heterorthisina* differs from *Heterorthis* in lacking the widely divergent diductor scars in the ventral valve, and the thickened ridges parallel to the anterior margins. The deposition of adventitious shell about the cardinalia takes more the form of that seen in *Dalmanella* rather than that of *Heterorthis*. In the latter the brachiophore plates are thickened at their dorsal and distal extremities, the thickening being prolonged as curved margins around the adductor field. The cardinal process of *Heterorthis* is also different from that of *Heterorthisina*. The myophore of the former is elongated ventrally and the median lobe drawn out posteriorly into a rather sharp carina. The lateral lobes are reduced to small ridges or bosses. In *Heterorthisina*, on the other hand, the process is small, bilobed, and cleft in front, as seen commonly in *Dalmanella*. No trace of a heterorthisoid chilidium was seen in *Heterorthisina*. The internal structure of the genus relates it more closely to *Dalmanella* than to *Heterorthis*, and for this reason we are placing it in the family Dalmanellidæ.

GEOLOGIC RANGE.—Upper Ordovician of Europe and possibly of the Ohio Valley.

EUROPEAN SPECIES

Heterorthisina præculpta Bancroft 1928

Orthis ellipsoides Barrande 1847

AMERICAN SPECIES

? *Dalmanella fairmountensis* Foerste 1909

Family WATTSELLIDÆ Schuchert and

Cooper 1931

Progressive and terminal Dalmanellacea originating in the Dalmanellidæ, with subcircular or shield-shaped shells, cordate ventral muscle field, and fulcral plates defining the sockets.

GEOLOGIC RANGE.—Upper Ordovician to Lower Devonian.

Embraces the following genera:

Wattsella Bancroft

Resserella Bancroft

Horderleyella Bancroft

Mendacella Cooper

Idiorthis McLearn

Parmorthis Schuchert and Cooper

Fascicostella Schuchert and Cooper

The genetic relations of the Wattsellidae appear to be as shown in Table 10.

Genus WATSELLA Bancroft 1928

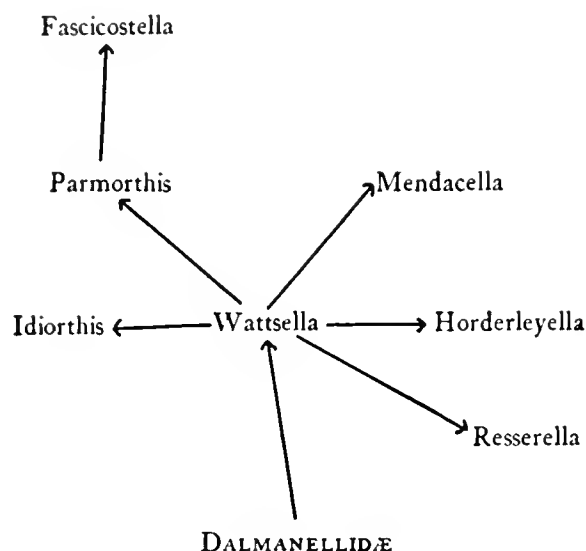
Pl. 22, figs. 9, 13, 14, 17-29

Bancroft, Mem. Proc. Manchester Lit. and Philos. Soc., vol. 72, 1928, p. 55, pl. 1, figs. 1-5.

GENOHOLOTYPE.—*WattSELLa wattSi* Bancroft 1928.

DESCRIPTION. *Exterior*.—Subcircular, hinge-line straight, narrower than the greatest width of the shell; cardinal extremities rounded; lateral profile unequally biconvex, the ventral valve always with the greater

Table 10



convexity. Anterior commissure rectimarginate to faintly sulcate. Dorsal sulcus shallow, deepest posteriorly; ventral fold conspicuous only at the posterior. Ventral palintrope longer than the dorsal, curved, apsacline, beak incurved, umbo strongly convex. Dorsal palintrope short, faintly anacline, beak inconspicuous; umbo sulcate, delthyrium and notothyrium open. Surface multicostellate; shell fibrous, punctate.

Ventral interior.—Delthyrial cavity deep; teeth strong; crural fossettes deep; dental plates sharp, divergent, commonly continued forward as a ridge on the lateral periphery of the diductor scars. Muscle area subcordate, more or less gently bilobed in front. Adductor track linear, squarish in front. Diductor scars elongate, rounded in front, and narrowing behind; adjustor scars not separable.

Dorsal interior.—Cardinalia prominent, brachio-phores elongated into slender points, extending nearly directly ventrally; brachio-phore supports triangular in side view, convergent, and uniting with the median ridge; sockets defined by a small fulcral plate. Car-

dinal process small; shaft slender, and only defined in the space between the brachio-phore supports; myo-phore lobed. Median ridge prominent, extending to the middle of the valve; muscle area oval, widest in front. Anterior adductor scars the larger.

GEOLOGIC RANGE.—Upper Ordovician into early Silurian.

AMERICAN SPECIES

Dalmanella edgewoodensis Savage 1913

Shells of this genus are common in eastern North America and are now parading as *Dalmanella testudinaria*

EUROPEAN SPECIES

Orthis testudinaria Dalman 1828

Terebratula unguis Sowerby 1839

WattSELLa wattSi Bancroft 1928

? *W. multiplicata* Bancroft 1928

DISTINGUISHING CHARACTERS.—This genus differs from *Dalmanella* in its more cordate muscle area, the subparallel brachio-phore supports which converge dorsally to meet the median ridge, the presence of fulcral plates defining the socket, and the exceedingly long tenuous brachio-phores.

DISCUSSION.—In restricting *Dalmanella* to shells of the type of *Orthis rogata* Sardeson, which Hall and Clarke mistakenly identified as *Orthis testudinaria* Dalman, the writers have left the European dalmanellid group without a proper generic name. Bancroft's recently proposed *WattSELLa* has a structure identical with that of *Orthis testudinaria* Dalman and must therefore include that species. Bancroft laid generic value on the differences in the cardinalia of the dalmanellids and based several genera on their variations.

The cardinalia of *WattSELLa*, as well as the ventral musculature, are strikingly different from those of *Dalmanella* as restricted by us. In the latter genus the diverging brachio-phores are typically bladelike, and are never provided with fulcral plates defining the socket. In *WattSELLa*, on the other hand, the brachio-phore plates converge dorsally to meet the outside margins of the median ridge. It is these plates that make the parallel slots in internal molds (see pl. 22, fig. 20). The median ridge extends to the middle of the valve, is low and wide. The cardinal process is normally rather small, with a short shaft and trilobed myophore which in its lateral lobes in adults or old forms may be extended anteriorly some distance. When such is the case, it gives this structure the appearance of being fissured. In some specimens the median lobe may be extended forward along the shaft as in *Isorthis*, so that the cardinal process simulates in form the head of a bee or fly.

In mature forms of *WattSELLa*, as in most other genera of the Dalmanellacea, adventitious shell is deposited about the brachio-phore plates. In the genus

under discussion, this secondary shell is deposited mainly between the brachiophore plates in connection with the cardinal process, but in *Orthis testudinaria* Dalman from Borensult, Sweden, the brachiophores are swollen on the inside at their junction with the median ridge and a very noticeable amount has also been deposited in the cavities between the brachiophore and the fulcral plates. If this deposition were carried to its extreme, the fulcral plates would be obliterated and the cardinalia would simulate those of *Dalmanella*, *Levenea*, and other genera of the Dalmanellidæ.

In the ventral valve the differences are not so striking. However, the diductor scars are not so long and flexuous, and the muscle impressions as a whole are more heart-shaped than in *Dalmanella*.

Wattsella is abundant in the Upper Ordovician of England and Wales and in the early Silurian of Sweden in strata previously regarded as Ordovician. In the United States, it is known for the first time in the early Silurian (Edgewood limestone of the Alexandrian series) of Illinois and Missouri. This is a striking fact which lends strength to the assertion made in the discussion of *Dalmanella*, namely, that shells having the structure of *Orthis testudinaria* Dalman are as yet unknown in the North American Ordovician. In the Silurian of Arisaig some of the specimens referred by McLearn⁹⁷ to *Dalmanella elegantula* actually belong to *Wattsella*. It is not improbable that some of the Silurian dalmanellids from Anticosti referred to *D. testudinaria* by Twenhofel will prove to be *Wattsellas* when the interiors are studied. Further, many of the "Dalmanellas" collected by Williams in the Silurian of Maine prove to belong to Bancroft's genus.

Genus *RESSERELLA* Bancroft 1928

Pl. 17, figs. 14-16

Bancroft, Mem. Proc. Manchester Lit. Philos. Soc., vol. 72, 1928, p. 54.

GENOLECTOTYPE.—*Orthis canalis* Sowerby 1839, in Murchison, Sil. Syst., pl. 13, fig. 12a.

DESCRIPTION. — Externally, *Resserella* (as here restricted) forms a very precise homœomorph of *Dalmanella* as described in this memoir. The valves are unequally biconvex, the dorsal being flatly convex and the ventral rather strongly so. There is a shallow sulcus on the dorsal valve that is defined from the vicinity of the beak to the anterior margin. The beaks and the interareas have the same features exhibited by *Dalmanella s. s.* The external surface is multicostellate as in the American shells.

Inside the ventral valve the identity with *Dalmanella* is carried out to the form and lobation of the muscle area. In the dorsal valve the cardinalia of mature shells are identical with mature *Dalmanella*.

In *Resserella* the adductor impressions of the dorsal valve are subequal and form a rather circular pattern.

DISCUSSION.—From the above it will be seen that the interior and exterior of *Resserella* and *Dalmanella* are very close if not identical in mature shells. For this reason we had regarded *Resserella* as a synonym of *Dalmanella* (restricted) in the early phases of our work. However, in correspondence with Mr. Bancroft, he has assured us that there is a very close relationship between *Resserella* and *Wattsella*, to be seen in the presence of fulcral plates in the early growth stages of the former. If these fulcral plates exist in *Resserella*, we admit the validity of the genus. We have not seen such plates in the material available to us and must accept Bancroft's statement.

The recognition of *Resserella* as a distinct genus does not invalidate our genus *Parmorthis*, based on *Dalmanella elegantula*, which Bancroft places in his *Resserella*. The type selected by Bancroft for his genus is *Orthis canalis* of Sowerby. As originally described, this species was composite, including within it Ordovician and Silurian specimens. On the basis of the latter, Davidson made Sowerby's species a synonym of *Orthis elegantula* Dalman. The specimen from the Ordovician, however, according to Sowerby's figures and remarks (pp. 630, 640), is different from the Silurian forms, which clearly belong to "*Dalmanella*" *elegantula* (Dalman) and were so referred by Davidson. On the other hand, specimens sent us by Mr. Bancroft prove to be of the larger Ordovician form, and it is on this shell and not on the "*elegantula*" type that *Resserella* is based.

Resserella as thus restricted consists of shells that are more circular as a rule than those of *Parmorthis*. Furthermore, the species of the latter genus have a rather definite ribbing system unknown in *Resserella*, consisting of a rather prominent median fascicle in both valves that is so well developed in some of the species as to produce a flattened or smooth portion in the middle of the valves at the front. On the interior, however, the differences between *Resserella* and *Parmorthis* are still more pronounced. In the ventral valve the strong arching of the beak produces a very deep delthyrial cavity and strong dental plates, much thicker than those of *Resserella*. Moreover, the ventral muscle field of *Parmorthis* is not decidedly lobate as is the corresponding area in *Resserella*. Inside the dorsal valve the differences are equally striking. In *Resserella* as known to us there is no prominent thickening produced laterally along the periphery of the adductor field, whereas this same area in *Parmorthis* has a very distinctive shape shared only by the closely related *Fascicostella*. Here the adductor area is elongate and the anterior impressions are triangular. Another very important difference between the two genera is the striated teeth and sockets of *Parmorthis*, which are very rare in the whole brachiopod class.

It is clear, therefore, that *Resserella* and *Parmorthis*

⁹⁷ Geol. Surv. Canada, Mem. 137, 1924, pp. 53-54.

are quite distinct. There are also notable differences between *Resserella* and *Wattsella*, particularly in the ribbing characters. We are, however, willing at present to accept Mr. Bancroft's statement regarding the relationships of these two genera in the absence of specimens of immature *Resserella*.

Genus *HORDERLEYELLA* Bancroft 1928

Pl. 22, figs. 30, 32-35

Bancroft, Mem. Proc. Manchester Lit. Philos. Soc., vol. 72, 1928, p. 178, pl. 1, figs. 15-18.

GENOHOLOTYPE.—*H. plicata* Bancroft 1928.

DESCRIPTION. *Exterior*.—Shells rather small, sub-semielliptical or subquadrate in outline; hinge-line straight, cardinal extremities obtuse. Lateral profile subequally biconvex. Anterior commissure sulcate, sulcus shallow; ventral fold subcarinate. Interareas subequal, ventral one apsacline, dorsal anacline. Ventral umbo rather strongly convex, dorsal umbo gently convex. Surface strongly fascicostellate. Test probably punctate.

Ventral interior.—Delthyrial cavity rather deep; dental plates short and strong; muscle area short, sub-pentagonal; diductor impressions subtriangular. Adductor impression linear, occupying a depression formed by the posterior extension of the fold. Pallial impressions unknown.

Dorsal interior.—Notothyrial cavity shallow, brachiophores long, brachiophore plates convergent dorsally and uniting with the median ridge. Sockets defined by fulcral plates.

GEOLOGIC RANGE.—Ordovician of England and Wales. The species are: *H. plicata* Bancroft, *H. n. sp.*

DISCUSSION.—This genus was originally placed by its author in the Harknessellinae, but it appears to us to belong nearer *Wattsella*, since its brachiophores are supported by convergent plates and there is a fulcral plate bounding the socket. From *Wattsella* it differs in the greater convergence of the brachiophore supports, which do not appear as parallel slits in internal molds.

Genus *MENDACELLA* Cooper 1930

(Lat. *mendax*, lying)

Pl. 22, figs. 1-5, 8

Cooper, Jour. Pal., vol. 4, 1930, pp. 377, 380, pl. 36, figs. 2, 16-18 (*uberis*), also figs. 6, 9 (*mullochiensis*).

GENOHOLOTYPE.—*Orthis uberis* Billings 1866, Cat. Sil. Foss. Anticosti, p. 42.

DESCRIPTION. *Exterior*.—Similar to *Rhipidomella* but with the valves subequally convex. The ventral valve is always the larger of the two.

Ventral interior.—Delthyrial cavity moderately deep; teeth large; dental plates strong, subparallel or divergent, continued forward as ridges on the outer margins of the diductor scars. Muscle area bilobed in front; diductor scars long and narrow; adductor ridge wide or narrow, carinate or flat, never extended to the front of the diductor scars. Adjustor scars small or large, narrow. Pallial markings not observed.

Dorsal interior.—Cardinalia confined; brachiophores stout, bluntly pointed, slightly divergent; sockets deep, defined by a small concave fulcral plate. Cardinal process small, shaft slender, not extending anterior to the ends of the brachiophore plates, myophore expanded lobate; a low broad median ridge extending from the ends of the brachiophore plates nearly to the middle of the valve. Adductor scars subequal, separated in some species by low ridges at right angles to the median ridge.

GEOLOGIC RANGE.—Upper Ordovician and early Silurian.

AMERICAN SPECIES

Orthis æquivalvis Shaler 1865 = *O. uberis* Billings 1866

Rhipidomella rhynchonelliformis (Shaler) 1865

Schizophorella arisaigensis McLearn 1924

? *Rhipidomella circulus* (Hall) 1843

? *R. lenticularis* Foerste 1903

? *R. tenuilineata* Foerste 1913

EUROPEAN SPECIES

Orthis minuscula Barrande

O. mullochiensis Davidson (Sil. Brach., p. 221)

DISTINGUISHING CHARACTERS.—This genus is distinguished especially by the *Dalmanella*-like character of the interior and the *Rhipidomella*-like exterior. Externally, however, it differs from *Rhipidomella* in having the ventral valve usually the larger. Internally the variations of the muscle-scars, dental plates, and cardinalia from those of *Rhipidomella* are striking. The muscle area does not have the broadly semiflabellate diductor scars enclosing the oval adductor ones. The diductor impressions of *Mendacella* are quite direct and narrow, and ordinarily only slightly divergent; they have a rather strong resemblance to the same scars in *Dalmanella*.

DISCUSSION.—There is some variation in the ventral musculature between the various species placed by us in this genus. In *M. uberis* from the Ellis Bay formation (late Ordovician) the diductors are frequently separated by a low wide ridge, but in the same species from the Silurian Gun River formation the ends of the diductors are separated from each other by a very narrow ridge only. The other Silurian species such as *M. arisaigensis* and *M. mullochiensis* all resemble the Silurian *M. uberis* in this respect. There is also a variable development of the adjustor scars within the same species and in different species.

From the structure of the cardinalia with its moderately divergent brachiophore plates, strengthened by fulcral plates, it is to be deduced that *Mendacella* is more closely related to *Wattsella* and *Parmorthis* than to *Dalmanella* and its allies.

Genus IDIORTHIS McLearn 1924

Pl. 21, figs. 34-38

McLearn, Geol. Surv. Canada, Mem. 137, 1924, p. 56, pl. 3, figs. 19-24, pl. 4, figs. 1-4, pl. 28, fig. 10.

GENOHOLOTYPE.—*I. matura* McLearn 1924.

DESCRIPTION. *Exterior*.—Suborbicular, hinge-line narrow, cardinal extremities rounded; lateral profile plano- to concavo-convex, the dorsal valve usually convex at the umbo but flat or concave in front of the middle. Anterior commissure slightly sulcate; ventral interarea the longer, curved, apsacline; beak incurved; delthyrium open. Dorsal interarea short, anacline. Ornamentation multicostellate. Test punctate.

Ventral interior.—Delthyrial cavity deep; teeth strong; dental plates thick, divergent, continued as ridges around the periphery of the diductor scars. Muscle field cordate, occupying nearly half the length of the valve. Diductor scars large, irregularly subtriangular, longer than the adductor track which is elongate, rectangular; adductor scars elliptical; adjustor scars not visible, or very narrow and situated at the base of the dental plates.

Dorsal interior.—Cardinalia ponderous, brachiophores and their supporting plates not separable, subparallel or slightly divergent. Cardinal process trilobed, its shaft obscured by the median ridge which is thick and clavate posteriorly but tapers to a point toward the front and terminates at the margin of, or just in front of, the anterior end of the muscle field. Muscle area reduced by the encroachment of the crural base supports which have forced the posterior adductors "up on the truncated anterior face of the crural lamellæ, which, expanding laterally, curve around the postero-lateral borders of the greatly enlarged and almost circular anterior adductor scars" (McLearn).

GEOLOGIC RANGE.—Early and ? Middle Silurian.

AMERICAN SPECIES

Idiorthis avita McLearn 1924

I. matura McLearn 1924

EUROPEAN SPECIES

? *Orthis edgelliana* (Salter MS.) Davidson (Sil. Brach., p. 228)

DISTINGUISHING CHARACTERS.—These are the extremely large ventral muscle area, strong divergent dental plates, subparallel arrangement of the brachiophore supports, large size and structure of the median

ridge and cardinal process, and nature of the dorsal musculature. These characters are combined with a concavo-convex exterior.

DISCUSSION.—*Idiorthis* most closely resembles *Wattsella* in the internal structure of the valves. The ventral muscle field is obcordate as in the former genus, with a rather wide adductor track. In the dorsal valve the brachiophore plates, situated on each side of the median ridge, are subparallel. The sockets appear to be defined by small socket-plates. The encroachment of the adductor muscles upon the front ends of the brachiophore supports in the type specimens is due to their being gerontic individuals. This fact also accounts for the peculiar structure of the cardinal process and the median ridge. Accordingly it is our view that *Idiorthis* as now understood is an old-age stage of *Wattsella*, but in the absence of young specimens this can not be proved.

Idiorthis has not been identified outside of the Arisaig section but McLearn has suggested a resemblance of *Orthis edgelliana* Salter to its genotype.

Genus PARMORTHIS Schuchert and Cooper 1931

(Gr. *parme*, shield)

Pl. 21, figs. 1-16, 29

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 246.

GENOHOLOTYPE.—*Orthis elegantula* Dalman 1828, K. Svensk. Vet. Akad. Handl. f. 1827, p. 117, pl. 2, fig. 6.

DESCRIPTION. *Exterior*.—Suborbicular, elongate elliptical or shield-shaped in outline; margins convex, front margin frequently slightly produced; hinge-line narrower than the greatest shell width; cardinal extremities rounded; lateral profile plano-convex, ventral valve ventricose, dorsal valve with a shallow sulcus; ventral interarea strongly curved, slightly apsacline, umbo swollen, beak strongly curved; dorsal interarea short, anacline, beak nearly obsolete; delthyrium usually open, notothyrium closed by the cardinal process. Multicostellate, rarely fasciculate. Test punctate.

Ventral interior.—Delthyrial cavity deep; teeth ponderous, crenulated on the inner surface; crural fossettes deep; accessory socket large; dental plates strong, vertical, subparallel or only slightly divergent; muscle area confined to the delthyrial cavity; adductor track usually narrow, linear, slightly elevated; diductor scars triangular, not extended appreciably anterior to the adductor track, covering the walls of the delthyrial cavity; adjustor impressions narrow; a slight median thickening extends anteriorly from the adductor track, and on each side of this ridge and

closely adjacent to it, a pallial trunk runs forward nearly to the anterior margin.

Dorsal interior.—Cardinalia confined; brachio-phores large, divergent, bearing long blunt points given off from the inside antero-ventral part; sockets very deeply defined on the inner side by the sloping crenulated outer face of the crural base and a small concave fulcral plate which unites the brachio-phore to the floor of the valve. Denticle large; muscle area elongate-oval in outline; anterior adductors the smaller; peripheral ridges low; cardinal process small, bilobed or trilobed, shaft produced forward to the line of division between the diductors, where it is cleft.

GEOLOGIC RANGE.—Silurian.

AMERICAN SPECIES

Dalmanella concavoconvexa Twenhofel 1928

D. springfieldensis Foerste 1917

D. waldronensis Foerste 1917

Parmorthis crassicostata, n. sp.

? *Orthis media* Shaler 1865

EUROPEAN SPECIES

Orthis basalis Dalman 1828

O. elegantula Dalman 1828

O. visbyensis Lindström 1860

DISTINGUISHING CHARACTERS.—This genus is distinguished externally by its plano-convex contour, strongly inflated ventral valve, and peculiar ornamentation. Internally, the stout brachio-phores with their blunt processes, oval muscle area, unusual articulating apparatus with its crenulated teeth and sockets, and ventral muscles and pallial sinuses all combine to individualize the genus. From *Dalmanella s. s.*, *Parmorthis* is differentiated by its more inflated ventral valve, different ornamentation, differently shaped ventral muscle area, divergence of the brachio-phore plates at their junction with the floor of the valve, and possession of a concave fulcral plate. It differs from *Isorthis* in not possessing a complicated pallial system and in certain details of the cardinalia.

DISCUSSION.—There is a feature of the ornamentation of these shells which is characteristic. In the sulcus of the dorsal valve there is usually a concentration of costellæ due to the accelerated appearance of secondary and tertiary ribs. This frequently produces a nearly smooth or nearly plane area in the front of the sulcus that is ordinarily elevated as a slight fold in its center. There is a corresponding smooth area in the median portion of the ventral valve which is commonly depressed slightly below the general level of the shell. This peculiarity occurs in nearly all of the species studied.

The articulation of *Parmorthis* is unusual for the strength of its parts and their specialization. It is the only genus known among the orthids (except *Tropidoleptus*, now placed in the Dalmanellacea) that possesses

crenulated teeth and sockets. The details of the articulation are described on page 25.

Noteworthy also in this genus is the occurrence of a small deposit of secondary shell in the apex of the delthyrium. This has nothing whatever to do with a deltidium, being merely an apical callus such as occurs commonly in some spiriferid genera. In the dorsal valve the brachio-phores not uncommonly bear elongate, bluntly pointed processes on their inner dorsal and distal extremities. If these and similar processes occurring in the same position in other orthid genera could be homologized with the crura of the rhynchonellids, it would be possible to prove that the brachio-phores in reality are the same as the crural bases.

"*Dalmanella*" *visbyensis* (Lindström) shows an interesting variation from the usual type of *Parmorthis*. In this form the ventral beak is more strongly arched than is usual, actually overhanging the dorsal interarea. Along with this variation goes a concave dorsal valve. Within the dorsal valve the myophore of the cardinal process is directed backward (posteriorly and dorsally) so far as to be visible from the dorsal side. Seen from the inside, one perceives that the inner margins of the shaft and the brachio-phore plates are grown together.

Orthis elegantula Dalman differs importantly from our *Dalmanella* and from *Resserella*. In *Dalmanella* the ventral muscle field is lobate and the pallial markings widely divergent, whereas in *Parmorthis* the ventral pallial markings are closely appressed and subparallel, and the muscle area is never lobate and is confined to the delthyrial cavity. In the dorsal valve important differences also occur. The adductor field of *Parmorthis* is elongate, and in our *Dalmanella* it is subcircular. Further, the sockets of *Parmorthis* are defined by concave fulcral plates, which are lacking in *Dalmanella*. These differences we regard as of sufficient importance to separate the two genera and place them in different families.

Parmorthis crassicostata, n. sp.

Pl. 21, figs. 4, 5

Shell rather small, subcircular, of the type of *P. elegantula* but having rather coarse ribs, there being about 34 to the valve. Measurements of the holotype: length, 9 mm.; width, 9 mm.

Holotype, Cat. No. 913, Schuchert Collection, Yale University. Silurian (Niagaran), Martin's Mills, western Tennessee.

Genus FASCICOSTELLA Schuchert and Cooper 1931

(Lat. *fascis*, bundle; *costella*, a little rib)

Pl. 22, figs. 6, 7, 10-12, 15, 16, 31

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 246.

GENOHOLOTYPE.—*Orthis gervillei* Defrance 1827, Dict. Sci. Nat., vol. 51, p. 152.

DESCRIPTION. *Exterior*.—Dalmanelloid, subcircular to subquadrate; lateral profile plano- to slightly concavo-convex; anterior commissure rectimarginate or sulcate; sulcus on the dorsal valve shallow; ventral interarea curved, beak incurved; dorsal interarea anacline; ornamentation strongly fascicostellate, the chief distinguishing feature of the genus.

Ventral and dorsal interior.—Essentially the same as in *Orthis elegantula* Dalman (*Parmorthis*).

GEOLOGIC RANGE.—Upper Silurian ? to Lower Devonian of Europe, with the following species:

- Orthis dorsoaplicata* Béclard
O. gervillei Defrance
O. sedgwicki D'Archiac and Verneuil

DISCUSSION.—*Fascicostella* is distinguished from all other Dalmanellacea by its peculiar ornamentation, since it has the greatest development of fasciculation seen in any orthid. Internally the species most closely resemble *Parmorthis elegantula* of Gotland. However, the hinge-line is proportionately wider and the cardinal extremities less rounded and the ventral valve never so ventricose. The ventral musculature is like that of *P. elegantula*, but has larger adjustor scars. The pallial sinuses are also like those of the Gotland species in being closely together, subparallel, and separated by a narrow, low ridge. The anatomy of the dorsal valve agrees closely with that of *P. elegantula*.

The close similarity of the internal anatomy of *Fascicostella* to that of *Parmorthis elegantula* suggests that the genus had its origin in that form. *Fascicostella* seems to be localized in the Lower Devonian of Europe, except for Kozłowski's report⁹⁸ of "*Dalmanella*" *gervillei* in the highest Silurian of Poland (Borszczów).

Family BILOBITIDÆ Schuchert and Cooper 1931

Aberrant, specialized Dalmanellacea originating in the Dalmanellidæ, having an emarginate anterior margin, narrow hinge-line, and a deep sulcus in each valve.

The only genus is *Bilobites* Linnæus, extending from the Upper Ordovician into the early Middle Devonian of Europe and North America.

Genus BILOBITES Linnæus 1775

Linnæus, Syst. Nat., ed. Müller, vol. 6, 1775, p. 325.
 Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, p. 204, pl. 5B, figs. 11-14.
 Syn. *Dicælosia* King 1850.

GENOHOLOTYPE.—*Anomia biloba* Linnæus 1767, Syst. Nat., 12th ed., p. 1154.

DESCRIPTION. *Exterior*.—Small, bilobed, anterior margin emarginate, hinge-line narrower than the greatest width of the shell; lateral profile unequally biconvex; anterior commissure broadly sulcate. Ventral interarea the longer, curved, apsacline, umbo swollen, sulcate, beak incurved; dorsal interarea short, anacline, beak projecting slightly, incurved; surface multicostellate; shell coarsely punctate.

Ventral interior.—Umbonal cavity deep; teeth strong; dental plates thick and rather obscure; muscle area bilobed, thickened along the margins; divided centrally by a sharp ridge corresponding to the external sulcus; diductor scars semiflabellate, divergent, not enveloping the adductor impressions; adductor scars borne on the central ridge, obscure; adjustor scars obscure.

Dorsal interior.—Cardinalia thick, brachiophores ponderous, long, bladelike, widely divergent; sockets shallow; cardinal process thick; myophore bilobate, crenulated on its posterior face, its shaft extended forward and merging with the median ridge formed by the impression of the external sulcus on the inside of the shell.

GEOLOGIC RANGE.—Upper Ordovician (Whitehouse group of Girvan; Richmondian of Gaspé, Quebec); widely in the Silurian; Lower Devonian (New Scotland, United States) and early Middle Devonian (Bohemia, G₁).

AMERICAN SPECIES

- Bilobites acutilobus* (Ringueberg) 1888
B. bilobus (Linnæus) 1767
B. indentus Cooper 1930
B. varicus (Conrad) 1838

EUROPEAN SPECIES

- Bilobites bilobus* (Linnæus) 1767
B. verneuilianus Lindström
Orthis dimera Barrande

DISCUSSION.—External form most readily distinguishes *Bilobites* from all other genera of the Dalmanellacea. Internally the ventral musculature and cardinal process are decidedly dalmanelloid. The brachiophores appear to be modified dalmanelloid, bladelike, and suggest an origin out of *Dalmanella*. Beecher⁹⁹ has figured a deltidium perforated at the apex in young *Bilobites*, but such a structure has not been observed in any of the mature forms studied or in any other punctate shell. If this actually exists only in the young of *Bilobites*, it is one more crumb of evidence that a delthyrium covered by a deltidium is actually the primitive condition in early brachiopod

⁹⁸ Pal. Polonica, vol. 1, 1929, p. 70.

⁹⁹ Studies in Evolution, 1901, p. 402.

growth stages, as is so forcibly indicated by the occurrence in the early Cambrian of *Nisusia* and the later Billingsellidæ with their covered delthyria.

Beecher¹⁰⁰ has suggested the derivation of *Bilobites* "from a radicle having, in many respects, the characters of the group represented by *Platystrophia biforata*." This statement has been construed by Cumings¹⁰¹ and others as "a virtual demonstration of the derivation of *Bilobites* from *Platystrophia*." Beecher and Cumings showed the external resemblances between the nepionic stages of the two genera, but the former merely pointed out that the two may have come from a platystrophoid radicle. This is true from the standpoint of exteriors, but certainly the internal features of *Bilobites* and *Platystrophia* are diverse. On an earlier page it has

Genus MYSTROPHORA Kayser 1871

Pl. 16, figs. 1-5; t. figs. 20, 21

Kayser, Zeits. deut. geol. Gesell., vol. 23, 1871, pp. 612-614, pl. 13, fig. 5.

GENOLECTOTYPE (Williams and Breger 1916).—*Orthis areola* Quenstedt 1871, Petref. Deutschl., p. 589, pl. 57, fig. 27.

DESCRIPTION. *Exterior*.—Transversely subquadrate to subsemicircular in outline; cardinal extremities obtuse or angular; lateral profile plano-convex; anterior commissure sulcate, sulcus deep, ventral fold low, marked by a median costella. Ventral palintrope long, strongly apsacline, beak slightly curved; del-

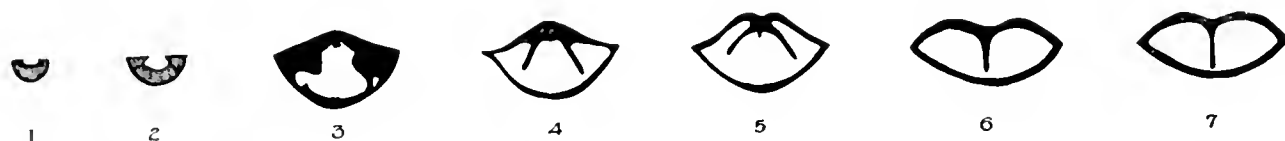


FIG. 20.—*Mystrophora areola* Quenstedt.—Section 1 shows the peculiar apical plate, which is punctate; 2 shows the relationship of this plate to the dental lamellæ; 4 and 5 show the long brachial processes; and the last two sections illustrate the strong median septum. Distance of sections from beak:

| | |
|-----------|-----------|
| 1—0.8 mm. | 5—4.7 mm. |
| 2—1.5 | 6—6.7 |
| 3—3.2 | 7—7.1 |
| 4—3.8 | |

The complete specimen was 10 mm. long. The median septum thus divides the shell into two chambers. x about 2.

been shown that *Platystrophia* is most closely allied to *Plectorthis* and *Hebertella*, that its cardinalia form a distinct type among impunctate orthids. The test of *Bilobites* is punctate and its whole expression is dalmanelloid. It would seem, then, that *Bilobites* has been derived from a dalmanelloid stock that introduced deep emargination of the anterior margin, a strong sulcus in each valve, and the enlargement of the primitive bladelike *Dalmanella* brachiophores. Accordingly any origin from *Platystrophia* is held to be untenable.

Family MYSTROPHORIDÆ Schuchert and Cooper 1931

Aberrant and specialized Dalmanellacea paralleling *Skenidioides* internally. The brachiophores form a cruralium and the cardinal process is lobate. The only certain genus of the family is *Mystrophora* Kayser, which appears to have had its origin in the Dalmanellidæ. We provisionally refer here also the genus *Kayserella*. Both genera are of the Middle Devonian of Germany.

thyrium usually open but may be closed at the apex by callus. Dorsal interarea short, plane, anacline; notothyrium partially closed by the cardinal process. Surface finely multicostellate; shell fibrous, punctate.

Ventral interior.—Delthyrial cavity deep; dental plates low, divergent. At the apex between the dental plates there is a flat callus deposit, probably for pedicle attachment. The cavity beneath this is usually completely filled by punctate shell substance.

Dorsal interior.—Notothyrial cavity deep; cardinal process with a long shaft and lobate myophore. Brachiophores elongate, pointed. Brachiophore supports convergent and uniting with a median septum, which is so high as to divide the shell into two chambers. Musculature unknown.

GEOLOGIC RANGE.—Middle Devonian.

EUROPEAN SPECIES

Orthis areola Quenstedt 1871

O. deshayesi Rigaux 1873

Scenidium fallax Gürich 1896 } Publication not seen

S. polonicum Gürich 1896

DISTINGUISHING CHARACTERS.—The name *Mystrophora* has usually been regarded as a synonym of *Skenidium*, despite the fact that its author showed that some of the shells to which he applied the name were

¹⁰⁰ Op. cit., p. 404.

¹⁰¹ Amer. Jour. Sci. (4), vol. 15, 1903, p. 40.

actually punctate. *Mystrophora*, however, differs so strongly from *Skenidium* in other details that it could easily have been determined as generically distinct without the aid of punctation. The lobate cardinal process, together with the punctation, at once establishes *Mystrophora* as a dalmanellid. It differs further from *Skenidium* in the ventral valve, which has no spondylium; instead, the divergent dental plates are attached directly to the floor of the valve. In the apex, growing to the inner sides of the dental plates, is a flat plate, probably for pedicle attachment, similar to that seen occasionally in *Schizophoria* and other members of the Schizophoriidæ.

DISCUSSION.—In describing *Mystrophora*, Kayser did not definitely designate a genotype. Underneath



FIG. 21.—*Mystrophora areola* (Quenstedt). Section about 2 mm. from the beak, showing relations of apical plate and dental lamellæ. \times ca. 12.

the heading "Subgenus *Mystrophora*" is placed a reference to Quenstedt's figures. At the end of his discussion, he names as typical species "*M. Lewisii* Davids." from the Silurian and "*M. areola* Quenst." in the order here given. Kozłowski¹⁰² makes the suggestion that if future work on *Skenidium* and *Mystrophora* should prove the former to be punctate, the name *Skenidium* could be used for the punctate species and *Mystrophora* with "*M. lewisii*" as the type for the impunctate group. In the absence of definite information one way or the other, he includes both punctate and impunctate forms under *Skenidium*.

It is clear from Kayser's text that he regarded *Orthis areola* as the type of his subgenus. This view was also held by Williams and Breger,¹⁰³ who say, "The type of *Mystrophora* was Quenstedt's *Orthis areola*." Schuchert and LeVene¹⁰⁴ more recently cite Quenstedt's species as the type, and it is so regarded in the present study.

Williams and Breger evidently considered *Mystrophora* a subgenus of *Dalmanella* in describing *D. (M.) elevata*. Their species is clearly a dalmanellid, and probably a *Wattsella* if one can depend on the ventral musculature.

Mystrophora is an aberrant and specialized dalmanellid paralleling *Skenidioides* in its internal dorsal

structure, but this feature has not yet evolved into the large hinge-plate of *Skenidium*.

Genus KAYSERELLA Hall and Clarke 1892

Pl. 16, figs. 7, 8, 10

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, p. 259, figs. 15-17.

GENOHOLOTYPE.—*Orthis lepida* Schnur 1853, Palaeontogr., vol. 3, p. 218, pl. 45, figs. 9a, b.

DESCRIPTION. *Exterior*.—Dalmanelloid, subcircular in outline; hinge-line narrower than the greatest width of the shell; cardinal extremities obtuse; lateral profile unequally biconvex, the ventral valve with the greater convexity; anterior commissure rectimarginate; dorsal valve provided with a shallow sulcus. Dorsal interarea long, nearly plane, strongly apsacline, beak very gently curved; delthyrium with elevated margins, partially covered by a convex deltidium; dorsal interarea short, anacline, notothyrium closed by the cardinal process and narrow chilidial plates. Surface multicostellate. Shell punctate.

Interior.—There was only one specimen of this genus in the Schuchert Collection, and sections of it proved disappointing because the shell is greatly mineralized. However, a few points regarding the internal structure were obtained. The delthyrial chamber is deep and surrounded by adventitious shell, which is also connected with the deltidium. Dental plates were not observed. In the dorsal valve the brachio-phores are long, but the brachio-phore plates could not be seen. The cardinal process is lobate as in other dalmanellids. Anterior to the cardinalia the median septum is extended so as nearly to touch the inner wall of the ventral valve, giving exactly the same appearance as in *Mystrophora*.

GEOLOGIC RANGE.—Middle Devonian of Germany.

DISCUSSION.—It has been customary for taxonomists to consider *Kayserella* a streptorhynchid, but, as Kozłowski¹⁰⁵ has pointed out, the shell is punctate exactly as in *Dalmanella*. This excludes the genus at once from *Streptorhynchus* and its allies, since, as this author has also shown, the Strophomenacea all have impunctate shells. Furthermore, the cardinal process is clearly dalmanelloid and not strophomenoid. These two characteristics, then—endopunctate shell and orthoid cardinal process—are sufficient to place *Kayserella* among the Dalmanellacea.

The genetic relations of the genus are not yet clear, but as it is best to refer it, on the basis of our present imperfect knowledge, to the family with which it most closely agrees, we place it provisionally with the Mystrophoridæ, though it probably does not belong here. We lay least family value on the sporadic reappearance of the deltidium and chilidium, and most on the internal features and the dalmanelloid exterior.

¹⁰² Pal. Polonica, vol. 1, 1929, pp. 46-47.

¹⁰³ U. S. Geol. Surv., Prof. Paper 89, 1916, p. 61.

¹⁰⁴ Foss. Cat., Pars 42, 1929, p. 86.

¹⁰⁵ Pal. Polonica, vol. 1, 1929, p. 89.

Family RHIPIDOMELLIDÆ Schuchert
1913, emended

(= partim Rhipidomellinæ Schuchert 1913)

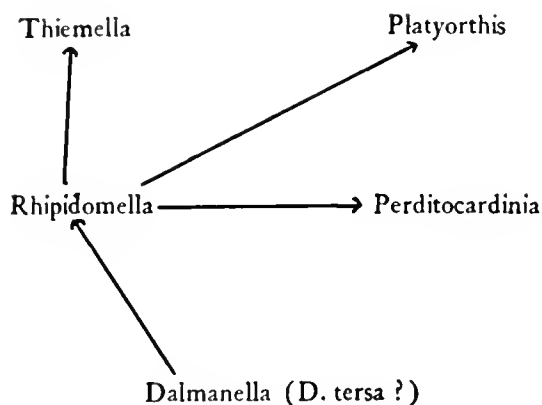
Subcircular, progressive, and terminal Dalmanella-
cea with broad flabellate diductor scars, completely
enclosing the elliptical adductor field in front. Brach-
iophores short, without fulcral plates.

This large family begins in the early Silurian and
dies out in the late Permian. It embraces the follow-
ing genera:

Rhipidomella Oehlert
Perditocardinia Schuchert and Cooper
Platyorthis Schuchert and Cooper
Thiemella Williams

The genetic relations seem to be as shown in Table
11.

Table 11



Genus RHIPIDOMELLA Oehlert 1890

Pl. 19, fig. 3; pl. 20, figs. 22-24, 26, 27

Oehlert, Jour. Conch. (3), vol. 30 [38], 1890, p. 372.
Hom. *Rhipidomys* Oehlert 1887.

GENOHOLOTYPE.—*Terebratula michelini* L'Eveillé
1835, Mém. Soc. Géol. France, vol. 2, p. 39, pl. 2,
figs. 14-17.

DESCRIPTION. *Exterior*.—Subtrigonal to circular,
anterior margin not uncommonly emarginate, hinge-
line narrow; lateral profile unequally biconvex, the
brachial valve having the greater convexity, with the
ventral one concave at the front in many species; an-
terior commissure faintly uniplicate or rectimarginate;
in some instances a sulcus on each valve; ventral
interarea the longer, curved, apsacline, umbo swollen
or gently convex, beak incurved; dorsal interarea
greatly reduced, ortho- to apsacline; delthyrium open,

notothyrium usually closed by the cardinal process or
partially by chilidial plates; surface multicostellate,
hollow costellæ numerous. Fibrous, punctate.

Ventral interior.—Delthyrial cavity shallow; dental
plates abbreviated, teeth strong, divergent, elongate;
a broadly curved ridge extending from the bases of the
low dental plates around the margin of the muscle
field; muscle field large, flabellate, not confined to the
delthyrial cavity, occupying from one-third to five-
sixths the length of the valve and usually deeply im-
pressed; diductor scars semiflabellate, separated from
each other by a sharp or low broad ridge, completely
enclosing the adductor scars, which form an elliptical
patch just anterior to the pedicle callist; adjustor scar
commonly discernible on the outside of the diductor
scar; pedicle callist occupying the delthyrial cavity.

Dorsal interior.—Cardinalia confined, sockets wide,
deep, without concave fulcral plates; brachiophores
long, bluntly pointed, supported by adventitious sub-
stance deposited beneath their anterior edge; sharp
processes or points on the ends of the brachiophores
have been interpreted as crura; cardinal process large,
myophore commonly ponderous, lobate; shaft short.
Median ridge extending to the middle of the shell.
Muscle field quadripartite, the posterior scars the
larger. Ovarian and pallial impressions occupying the
area of the shell not covered by the muscle marks.

GEOLOGIC RANGE.—Silurian (Clinton) to close of
Permian.

AMERICAN SPECIES

Rhipidomella alsa (Hall) 1863
R. altirostris Mather 1915
R. arkansana Girty 1911
R. assimilis (Hall) 1859
R. burlingtonensis (Hall) 1858
R. carbonaria (Swallow) 1858
R. clarkensis (Swallow) 1863
R. cleobis (Hall) 1863
R. cumberlandia (Hall) 1859
R. dalyana (Miller) 1881
R. diminutiva Rowley 1900
R. discus (Hall) 1859
R. dubia (Hall) 1858
R. ellsworthi Tansey 1922
R. emarginata (Hall) 1859
R. goodewini (Nettelroth) 1889
R. hessensis King 1931
R. hybrida (Sowerby) 1839 (now a composite species, in-
cluding forms referable to *Mendacella*)
R. idonea (Hall) 1867
R. intermedia Stauffer 1918
R. jerseyensis Weller 1914
R. lehuequetiana Clarke 1907
R. leonardensis King 1931
R. leucosia (Hall) 1860
R. livia (Billings) 1860
R. logani Clarke 1907
R. lucia (Billings) 1874
R. magnicardinalis Foerste 1909

AMERICAN SPECIES—*Cont.*

- R. melvillei* Tansey 1922
R. mesoplatys King 1931
R. mesoplatys baylorensis King 1931
R. minima Savage 1921
R. missouriensis (Swallow) 1860
R. musculosa (Hall) 1857
R. nevadensis (Meek) 1877
R. newsomensis Foerste 1909
R. oblata (Hall) 1857
R. occasus (Hall) 1860
R. oweni Hall and Clarke 1892
R. pecosi (Marcou) 1858
R. peloris (Hall) 1863
R. penelope (Hall) 1860
R. pennsylvanica (Simpson) 1889
R. perminuta Girty 1926
R. preoblata Weller 1903
R. saffordi Foerste 1903
R. semele (Hall) 1863
R. suborbicularis (Hall) 1858
R. tenuicostata Weller 1914
R. tenuilineata Savage 1913
R. thiemi (White) 1860
R. transversa King 1931
R. vanuxemi (Hall) 1857
R. vanuxemi pulchella (Herrick) 1888
R. variabilis Grabau 1913

FOREIGN SPECIES

- Rhipidomella altaica* Obrut. 1926
R. grandis Tolmachev 1912
R. harti (Rathbun) 1879
R. hybrida (Sowerby) 1839
R. imitatrix Diener
R. inca (D'Orbigny) 1842
R. michelini (L'Eveillé) 1835
R. penniana (Derby) 1874
R. polygramma (Sowerby) 1839
R. polygramma pentlandica (Davidson) 1868
R. reversa (McCoy)
R. subcordiformis Kayser

DISTINGUISHING CHARACTERS.—*Rhipidomella* is characterized externally by its nearly circular, or, in later species, subtrigonal outline; the unequal convexity of the valves, of which the dorsal is almost always the more ventricose, and the ventral one usually either markedly concave or showing a tendency in that direction. The hinge-line is always very narrow. Internally the ventral musculature is very characteristic and the teeth are different from those in nearly all other genera of the orthids. The dorsal valve, with its arched umbo, has a ponderous cardinal process with a very short shaft but an expanded myophore. The cardinalia are distinctive and consist of widely divergent brachiophores supported by inconspicuous deposits of adventitious shell much as in *Heterorthis*.

DISCUSSION.—The external variations of the shell are seen in outline and profile. Narrowing of the

hinge is frequently accompanied by a lengthening of the beak, producing thereby a subtrigonal outline. This outline is characteristic of most of the Pennsylvanian and Permian *Rhipidomellas*, but the Devonian shells, with few exceptions, are mostly quite orbicular. A fold and sulcus are rarely developed in true *Rhipidomella*, and when present are inconspicuous.

Internally there is a considerable variation in the ventral musculature but the essentials of the muscle pattern are uniform throughout the group. The most important character is the complete enclosure of the adductor scars by large semiflabellate diductor and adjustor impressions. The adductor scars are always situated at the posterior of the shell a short distance forward of the pedicle callist. The size and shape of the adjustor-diductor scar is very variable, "from one-third to five-sixths the length of the valve." It varies from circular to pentagonal and trigonal in outline. The most extravagant development of muscles is in *R. musculosa* in which nearly the whole floor of the valve is covered. It is very difficult to differentiate the adjustors from the diductors, but when this has been possible the adjustor scars are seen to be rather large. A median ridge usually divides the diductors medianly and a small extension of it passes posteriorly through the center of the adductor scar. This ridge may be sharp and septum-like or it may be in the form of a flat platform. It is not to be confused with the euseptoid of *Schizophoria* which is a sharp septum bearing the adductor scars.

The dorsal valve shows variation in the strength of the median ridge, which extends forward from the shaft of the cardinal process and divides the adductors medianly. Pallial marks are not commonly seen in *Rhipidomella*, but those of *R. emarginata* show two trunks, slightly divergent, extending forward from the antero-median ends of the anterior adductors. A lateral trunk extends from the ridges, dividing the adductors horizontally. These are elements similar to those observed in *Isorthis*.

The brachiophores are quite distinctive, being moderately long, rather thick, somewhat bladelike, and at the distal extremity are thickened or bear a toothlike process on their outer ventral surface. This denticle evidently serves to lock the tooth in place in the socket. The latter is wide, being merely the space between the brachiophore and the walls of the valve. Low flaring supporting plates of extra shell lend strength to the brachiophores. Additional strength is obtained by the deposition of adventitious shell on the inner surface of the brachiophores. Abbreviated chilidial plates are to be seen rarely.

Elongate blade- or spinelike processes extending from the distal extremity of the brachiophores are regarded by Hall and Clarke as crura. These processes are similar to others not infrequently seen in other orthid genera.

In some of the strongly biconvex Pennsylvanian *Rhipi-*

idomellas the brachiophores become much curved and extend ventrally rather than antero-ventrally as in the more normal species. This increase in depth to form globular shells among the late Paleozoic brachiopods is also repeated in *Enteleles* and *Meekella*.

Evidences of old-age features are to be seen in the overgrowth of the myophore and the great development of adventitious substance, especially about the brachiophores, in the umbonal cavities, and in thick deposits under the muscle fields in both valves.

The origin of *Rhipidomella* is to be looked for in *Dalmanella* of the Ordovician. In typical *Dalmanella* the diductors are long and slightly expanded in front, and the adjustor scars outside of them are well developed and prominent. The adductor impressions are central but not completely enclosed. In such a pattern are the fundamentals of the *Rhipidomella* ventral musculature. The transition is suggested by *D. tersa*, which is structurally intermediate between *Dalmanella* and *Rhipidomella*. *Rhipidomella* must have evolved from *Dalmanella* in the late Ordovician, as there are a number of early Silurian shells that already have the typical characters of *Rhipidomella*.

Subgenus PERDITOCARDINIA Schuchert and Cooper 1931

(Lat. *perdere*, to lose; *cardo*, hinge)

Pl. 19, figs. 12, 14-17, 20-22

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 246.

GENOHOLOTYPE.—*Orthis dubius* Hall 1858, Trans. Albany Inst., vol. 4, p. 12.

DISCUSSION.—In the St. Louis and Spergen limestones of Indiana, Illinois, Missouri, and Kentucky, there is a peculiar shell which is a distinct divergence from the main line of *Rhipidomella*, enough so to merit a subgeneric rank. This shell, *Orthis dubia*, differs from *Rhipidomella* in not having interareas or palintrope. The hinge-line has been narrowed to disappearance, with consequent obsolescence of the interareas. As a result, the shell is rostrate and suggests *Terebratulina* in external appearance. So far has the rostration gone that the ventral beak may be curved over the dorsal, enclosing it and obscuring it from view. With this rostration have also gone internal changes. The teeth resemble those of *Neothyris*, being attached to the floor and inner shell margin. In the dorsal valve the cardinal process, even in young forms, has become ankylosed with the brachiophores and their supporting tissue.

The rostration with resultant loss of interareas is not a gerontic characteristic, but is well defined in the earliest stages, showing that the evolution is well established. The one species thus far assigned to this subgenus is a composite, and it will probably prove desirable to separate it into several specific groups.

Genus PLATYORTHIS Schuchert and Cooper 1931

(Gr. *platys*, flat)

Pl. 19, figs. 18, 19, 23, 24, 27-29, 31

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 246.

GENOHOLOTYPE.—*Orthis planoconvexa* Hall 1859, Pal. N. Y., vol. 3, p. 168, pl. 12, figs. 1-6.

DESCRIPTION. *Exterior*.—Subcircular to elliptical, hinge-line narrow; lateral profile plano-convex, lateral commissure straight; anterior commissure rectimarginate; no fold or sulcus; ventral umbo swollen, interarea greatly reduced, nearly orthocline; beak strongly incurved, usually closely appressed to the margin of the dorsal valve; delthyrium open; dorsal interarea reduced nearly to disappearance; ornamentation multicostellate; test fibrous, punctate.

Ventral interior.—Delthyrial cavity deep; teeth strong, elongate, standing as ridges on the dental plates; crural fossettes deep; dental plates low and stout, widely divergent, produced forward as sharp ridges along the lateral margins of the diductor scars; muscle field large, flabellate, occupying more than half of the area of the interior; diductor scars elongate, semiflabellate, centrally divided by a low ridge; adductor scars elongate, oval, borne on a slight expansion of the median ridge.

Dorsal interior.—Cardinalia strong; brachiophores produced into a point at the distal extremity, brachiophore supports as in *Rhipidomella*, divergent, vertical, continued around the lateral margins of the muscle area as a thick ridge; cardinal process ponderous, ventro-centrally cleft, posteriorly bilobed but when viewed from the ventral surface appearing to be trilobed, its shaft produced for a short distance forward as a median ridge, which does not extend to the anterior margin of the muscle area; muscle field subquadrate, anterior adductor scars the larger.

GEOLOGIC RANGE.—Silurian to Middle Devonian.

AMERICAN SPECIES

Dalmanella lucia Clarke 1908

D. planoconvexa (Hall) 1859

EUROPEAN SPECIES

Orthis circularis Sowerby 1842

O. opercularis Verneuil 1845

Dalmanella cimex Kozłowski 1929

DISTINGUISHING CHARACTERS.—The chief distinguishing characters of *Platyorthis* are the plano-convex profile, dalmanelloid exterior combined with ventral muscle-scars and cardinalia like those of *Rhipidomella*, and a huge cardinal process. The brevity of the hinge-line, the lateral flaring of the dental plates, and the

character of the teeth are other important anatomical features of the genus.

DISCUSSION.—The members of *Platyorthis* have been variously referred to *Dalmanella* and *Rhipidomella*, but the combination of characters, both internal and external, makes this genus unique and distinguishes it from all other members of the Rhipidomellidæ or Dalmanellidæ. The cardinal process is notable for its extremely large size, a development that is probably the result of the flattening of the dorsal valve. The internal characters of *Platyorthis* ally it most strongly to *Rhipidomella*, and the group in all probability represents a deviation from the main *Rhipidomella* line. In Europe it appears in the Borszczów stage of the Silurian, occurs in the Siegener Schichten of the lower Coblenzian, and extends into the Middle Devonian (Eifelian). In America it is of Devonian time and ranges from the Becraft through the Oriskany and into the Grande Grève limestone of Quebec, which is lower Middle Devonian in age.

Genus THIEMELLA Williams 1908

Pl. 19, figs. 1, 2, 4-6, 9

Williams, Proc. U. S. Nat. Mus., vol. 34, 1908, p. 59, pl. 2, figs. 11, 12, 16, 19, 22, 23.

GENOHOLOTYPE.—*T. villenovia* Williams 1908.

DESCRIPTION. *Exterior.*—Like *Rhipidomella* except for the presence of a well marked ventral fold and an equally prominent dorsal sulcus. In young stages the fold and sulcus are reversed, and in mature and old forms both may become obsolete at the front.

Ventral interior.—Delthyrial cavity shallow, dental plates low, continued as a low ridge around the periphery of the muscle area, obsolete in old shells. Muscle field suboval to subcordate; diductor impressions subcrescentic, somewhat expanded in front; adjustor scars narrow. Adductor field an elliptical impression imprisoned by the diductor scars. Extending forward from the front end of the adductor field to beyond the middle of the valve is a low ridge. Lateral spaces coarsely pustulose.

Dorsal interior.—Cardinalia abbreviated and delicate; brachiophores as in *Rhipidomella*, divergent plates attached to the inner surface of the valve. Cardinal process with a short shaft, and the myophore a lobate boss on the notothyrial platform; median ridge low and obscure in adults. Adductor field confined.

GEOLOGIC RANGE.—Upper Devonian of eastern United States.

SPECIES

Thiemella villenovia Williams 1908

Dalmanella tenuilineata (Hall) 1843

? *Dalmanella danbyi* Williams 1908

? *Orthis leonensis* Hall 1867

DISTINGUISHING CHARACTERS.—*Thiemella* combines some of the generic features of *Schizophoria*, *Dalmanella*, and *Rhipidomella*. The external form is essentially that of *Rhipidomella*, but add to this a prominent dalmanelloid fold and sulcus, and the exterior is unlike that of any other dalmanellid except *Aulacella*. Williams named as one of the generic characters the reversion of the fold and sulcus from a ventral sulcus and dorsal fold in the young stages to a ventral fold and dorsal sulcus in mature forms. In many specimens, however, the fold and sulcus are lost at the front of the shell.

DISCUSSION.—*Thiemella* is closest to *Aulacella* of the Dalmanellidæ from the Eifelian of the Rhine. In this form the fold and sulcus are not reversed and internally there are other important differences from *Thiemella*. In the ventral valve of the latter the median ridge extending forward from the front end of the adductor field is undivided and continuous to beyond the middle of the shell. In the German genus, on the other hand, the low ridge dividing the diductor scars at the front is forked near the front margin of the diductor impressions. According to Williams, the "forked septum" is a feature characteristic of *Dalmanella* but in our experience it has proved not to have marked generic value.

In the dorsal valve the cardinalia of *Thiemella* are remarkable for their delicacy, whereas *Aulacella* has ponderous structures for so small a shell. These differences, when combined with the geologic age and geographic distribution, help to distinguish the two genera.

Family HETERORTHIDÆ Schuchert and Cooper 1931

Broad, flat or concavo-convex, divergent Dalmanellacea, having subflabellate ventral diductor impressions, not enclosing the adductor marks. Brachiophores like those of *Dalmanella*, cardinal process narrow, with an elongate myophore. In the cementation of the brachiophores to the floor of the valve, tissue is deposited under their dorsal surface and is not uncommonly continued anterior to the front ends of the brachiophores. This mode of cementation is not unlike that of *Rhipidomella* and suggests that the heterorthids may have arisen from the same stock of dalmanellids that gave rise to *Rhipidomella*.

The family is divided into the subfamilies Heterorthinæ Schuchert and Cooper and Harknessellinæ Bancroft. The genetic relations are apparently as shown in Table 12.

Subfamily HETERORTHINÆ Schuchert and Cooper 1931

Heterorthidæ with a plano-convex to concavo-convex lateral profile and without fold and sulcus. Has only the one known genus, *Heterorthis* Hall and Clarke.

Genus HETERORTHIS Hall and Clarke 1892

Pl. 20, figs. 16-21, 25; t. fig. 15

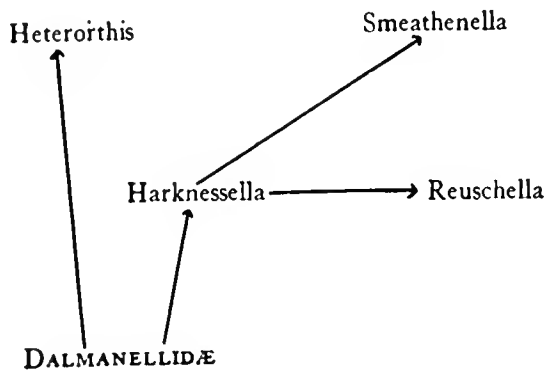
Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, pp. 202, 223, pl. 5b, figs. 20-24.

GENOHOLOTYPE.—*Orthis clytie* Hall 1861, 14th Rept. N. Y. State Cab., p. 90.

Table 12

HETERORTHINÆ

HARKNESSELLINÆ



DESCRIPTION. *Exterior*.—Rafinesquinoid, transversely subquadrate, margins convex, cardinal extremities rounded, hinge-line narrower than the greatest shell width; lateral profile depressed plano-convex to concavo-convex; anterior commissure rectimarginate; ventral interarea the longer, apsacline, delthyrium open, umbo expanded, beak incurved; dorsal interarea strongly anacline, notothyrium closed by the cardinal process or a small chilidium; ornamentation unequally multicostellate, swollen, hollow ribs numerous; shell fibrous, punctate.

Ventral interior.—Delthyrial cavity shallow; teeth strong, with sockets; dental plates short, flaring, obsolete in old forms; muscle area large; diductor scars widely divergent, elongate, semiflabellate, not enclosing the adductor impressions; adductor scar small, central; pedicle callist large; adjustor scars elongate, located at the base of the dental plates; around the inside margin of the valve is a thickened rim.

Dorsal interior.—Cardinalia confined; brachio-phore plates simple, bladelike, divergent, supported by

adventitious shell deposited at their bases. This secondary shell is prolonged for some distance into the valve. Sockets wide, deep. Muscle area subcircular; adductor scars subequal. Cardinal process large, shaft stout, not uncommonly covered by adventitious shell; myophore faintly lobate only at the ventral extremity, elliptical in section in the middle, carinate posteriorly. Dorsal extremity of myophore covered by a small chilidium. Pallial sinuses prominent, two trunks going forward from the anterior end of the median ridge, two obliquely from the antero-lateral margins of the anterior adductor, and a third pair laterally from the space between these muscles. In the dorsal valve there is also a thickening of the shell inside the margin.

GEOLOGIC RANGE.—Middle and Upper Ordovician of United States and Europe.

AMERICAN SPECIES

Heterorthis clytie (Hall) 1861

EUROPEAN SPECIES

Orthis alternata Sowerby 1839

O. inclyta Barrande 1879

O. retrorsistria McCoy 1852

Heterorthis barrandei, nom. nov. (defined below)

DISTINGUISHING CHARACTERS.—*Heterorthis* is distinguished from all other punctate orthids by its transversely subquadrate outline; depressed plano-convex or concavo-convex contour; widely divergent diductor scars and very small adductor impressions; confined, oblique brachio-phores; peculiar cardinal process; small convex chilidium; and thickened rim around the inside margins of both valves.

DISCUSSION.—The internal structure of the dorsal valve is probably just as characteristic of *Heterorthis* as are the elongate diductor scars in the ventral valve. The brachio-phore plates are small and bladelike as in *Dalmanella*, but are enlarged by secondary shell deposited at their bases and produced forward as a double-pronged hook. The myophore of the cardinal process is elongated ventrally and posteriorly, a modification that is probably due to the flatness of the valve and parallels *Platyrthis* in this respect. At the ventral extremity there is a slight trilobation of the myophore, indicating its derivation from a dalmanelloid stock. The trilobed effect is lost chiefly by the posterior prolongation of the central lobe into a prominent carina.

Most interesting is the chilidium, which is a rare feature in punctate orthids; it is a small, compressed, cup-shaped plate covering the postero-dorsal surface of the cardinal process. The chilidium takes its origin just inside the brachio-phore plates and its outer surface appears to be continuous with the interarea. This covering may have functioned as a protection to the muscle attachments on the median carina of the myophore.

Heterorthis is known from only one species in America but is better represented in continental Europe and Great Britain, where there are four forms. Bancroft¹⁰⁶ refers *Orthis patera* Salter (Davidson, Brit. Foss. Brach., vol. 3, pl. 30, figs. 1-8) to this genus but the musculature and pallial markings here are not those of *Heterorthis*. The species may belong to a new group, but is related to the heterorthids by the structure of the cardinalia and the general physiognomy of the shell. *Heterorthis* appears to be closely related to the members of the Harknessellinæ in the structure of the cardinalia and the musculature.

In the Bohemian fauna there is a shell figured by Barrande¹⁰⁷ which has the musculature of the ventral valve of *Heterorthis*. These two figures are referred to a new species which we name *H. barrandei*. *Orthis inclyta* Barrande also has widely divergent, semiflabelate diductor scars and is placed likewise in *Heterorthis*. In this species the adjustors are considerably more developed than in *H. alternata* and more than is usual in *H. clytie*.

Subfamily HARKNESSELLINÆ Bancroft

Heterorthidæ having biconvex valves, coarser ornamentation than is usual in the Heterorthinæ, a prominent fold on the ventral valve and an equally prominent sulcus in the dorsal. Embraces the following genera:

Harknessella Reed
Reuschella Bancroft
Smeathenella Bancroft

Genus HARKNESSSELLA Reed 1917

Pl. 20, figs. 6-10

Reed, Trans. Roy. Soc. Edinburgh, vol. 51, pt. 4, 1917, p. 862, pl. 11, figs. 3-7.

GENOHOLOTYPE.—*Orthis vespertilio* Sowerby 1839, Sil. Syst., pl. 20, fig. 11.

DESCRIPTION. *Exterior*.—Shell generally small or medium in size, usually subquadrate in outline; hinge-line straight; cardinal extremities acute or more rarely obtuse; lateral profile unequally biconvex, the dorsal valve usually having the greater convexity; anterior commissure sulcate; sulcus deep, ventral fold usually low but prominent. Ventral interarea longer than the dorsal, apsacline; umbo gently convex. Dorsal interarea prominent, moderately anacline, umbo gently convex. Surface costellate to fascicostellate. Shell punctate.

¹⁰⁶ Mem. and Proc. Manchester Lit. and Philos. Soc., vol. 72, 1928, p. 69.

¹⁰⁷ Syst. Sil. Bohême, vol. 5, pt. 1, pl. 66, fig. II, 11a and 14.

Ventral interior.—Delthyrial cavity shallow; teeth strong; dental plates short, widely divergent, continued as low ridges along the lateral margins of the muscle area. Muscle field subpentagonal, usually bilobed in front. Diductor scars elongate, usually extended in front of the anterior end of the adductor scar. Adjustor scars narrow, located at the base of the dental plates. Adductor scar elongate rectangular. Pallial markings obscure.

Dorsal interior.—Cardinalia heterorthoid, notothyrial cavity occupied by the cardinal process; brachiophores bladelike, cemented to the valve by adventitious shell deposited on their inside surface and dorsal edge. Cardinal process lobed, usually so overgrown as to appear simple; dorsal muscle impressions indistinct.

GEOLOGIC RANGE.—Upper Ordovician of Europe, with the following species:

Orthis vespertilio Sowerby 1839
Harknessella jonesi Bancroft 1928
H. subplicata Bancroft 1928
H. subquadrata Bancroft 1928

DISTINGUISHING CHARACTERS.—*Harknessella* is distinguished by the contour and profile of the valves, the subquadrate form being rather unusual in punctate shells. In the ventral interior the muscle-scars are dalmanelloid and in the dorsal the cardinalia suggest those of *Heterorthis*. This structural ensemble, combined with a fascicostellate exterior, makes a combination unique among the Dalmanellacea. The external form is similar to that of *Cariniferella* of the Upper Devonian.

DISCUSSION.—The greatest morphologic interest is in the dorsal valve and in the cardinalia. As stated above, the greatest similarity is with *Heterorthis*. In *Harknessella* the brachiophores are rather long, extending dorso-ventrally. They are unsupported except for adventitious shell deposited on the inside and along the dorsal edge, which unites them to the valve. This is similar to the condition in *Heterorthis*, but in *Harknessella* there is a much greater development of the notothyrial platform. This is usually swollen about the inside surfaces of the brachiophores, and in some instances the platform is nearly flush with the ventral edge of the brachiophores. In front of the notothyrial platform are two deep indentations separated by the median ridge; it is in these pits that the posterior adductor muscles were lodged. The cardinal process is distinctly lobed as in all Dalmanellacea but the shaft may be so swollen as to hide or obscure the original lobation. In one undescribed species the cardinal process is delicate, with a slender shaft but an expanded and lobed myophore.

The distinction between *Harknessella* and *Smeathenella* and *Reuschella* is rather difficult to see if one deals with either the actual shell or a wax replica thereof, but in internal molds is not so troublesome.

In *Harknessella* (see pl. 20, figs. 8, 9) the base of the brachiophores and their supporting tissue are triangular in plan, with the antero-lateral extremity of the triangle somewhat drawn out. The adductor pits are represented by two posteriorly directed acute lobes on each side of a median depression. Other differences are discussed farther on.

Harknessella is not uncommon in the Middle Ordovician (Caradocian) of the British Isles but is so far unknown in North America.

Subgenus REUSCHELLA Bancroft 1928

Pl. 20, figs. 11-15

Bancroft, Mem. and Proc. Manchester Lit. and Philos. Soc., vol. 72, 1928, p. 180, pl. 2, figs. 9-12, t. fig. 5.

GENOHOLOTYPE.—*R. semiglobata* Bancroft 1928.

DESCRIPTION. *Exterior*.—Shells commonly rather large, subquadrate in outline, hinge-line straight, cardinal extremities acute; lateral profile unequally biconvex or convexo-concave, the dorsal valve having the greater convexity. Anterior commissure more or less strongly sulcate; dorsal sulcus deep in young stages, obsolete or prominent in old stages; ventral fold subcarinate. Ventral interarea the longer, strongly apsacline; dorsal interarea anacline or orthocline. Umbos gently convex. Surface costellate to fascicostellate. Shell punctate.

Ventral interior.—Delthyrial cavity shallow; teeth strong; dental plates stout, flaring, rather short, continued as ridges on the lateral margins of the muscle area. Muscle field pentagonal in outline, gently bilobed in front. Adductor field linear, strongly impressed; diductor scars elongate, tear-shaped. Adjustor scars rather large. Pallial markings unknown.

Dorsal interior.—Notothyrial cavity obsolete, as it is filled completely by the notothyrial platform and the cardinal process; brachiophores bladeliike as in *Heterorthis*, cemented to the valve in front by adventitious substance. Sockets deep; cardinal process with a lobate myophore, shaft slender or swollen. Adductor impressions occupying troughs bounding the median ridge.

GEOLOGIC RANGE.—Middle Ordovician (Caradocian-post-Harnage) of the British Isles, with the following species:

- Reuschella bilobata* (Sowerby) 1839
- R. horderleyensis* Bancroft 1928
- R. semiglobata* Bancroft 1928

DISCUSSION.—*Reuschella* differs from *Harknessella* in its coarser ornamentation and in details of the cardinalia. Bancroft's description of this genus was made entirely from internal molds, and the distinctions from *Harknessella* that he points out and figures appear very slight. From specimens kindly sent to us by Bancroft we could discern no fundamental differences in the cardinalia. We recommend therefore that Bancroft's genus be considered a subgenus of *Harknessella*.

Genus SMEATHENELLA Bancroft 1928

Pl. 20, figs. 1-5

Bancroft, Mem. and Proc. Manchester Lit. and Philos. Soc., vol. 72, 1928, p. 177, pl. 2, figs. 1-5.

GENOHOLOTYPE.—*S. harnagensis* Bancroft 1928.

DESCRIPTION. *Exterior*.—Shell rather large, subquadrate in outline; hinge-line straight; cardinal extremities usually obtuse; lateral profile unequally biconvex or convexo-concave, the dorsal valve having the greater convexity. Anterior commissure sulcate; ventral fold strongly carinate. Interareas subequal, ventral interarea apsacline, dorsal anacline; umbos gently convex. Surface unequally costellate as in *Rafinesquina*.

Ventral interior.—Delthyrial cavity confined, shallow; dental plates short and stout, muscle area rhomboidal in outline.

Dorsal interior.—Like *Harknessella*; notothyrial cavity closed by the cardinal process and notothyrial platform. Brachiophore plates slender, heterorthoid. Sockets deep, median elevation corresponding to external large sulcus.

GEOLOGIC RANGE.—Middle Ordovician (Caradocian) of the British Isles, with the single species *S. harnagensis* Bancroft.

DISTINGUISHING CHARACTERS.—*Smeathenella* is very closely allied to *Harknessella* but differs in its ornamentation, lateral profile, and in details of the cardinalia. The ornamentation has been described by Bancroft as "markedly Rafinesquinoid," that is, there are coarser costellæ separated by many fine costellæ. This ribbing, in connection with a much less convex dorsal valve than is usual in *Harknessella* or *Reuschella*, will serve to distinguish the genus. Other differences setting apart this genus from the other two are to be found in the interior of both valves. The dental plates are usually proportionally shorter and the muscle field is smaller. In the dorsal valve the cardinalia are more slender and the adductor pits not as deeply excavated.

Family SCHIZOPHORIIDÆ Schuchert 1929

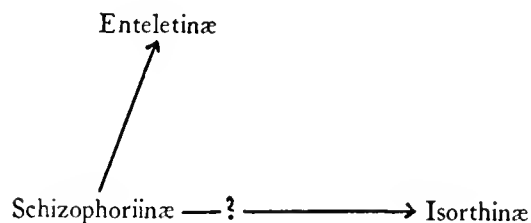
Progressive and terminal Dalmanellacea, probably derived out of the Dalmanellidæ,¹⁰⁸ having biconvex or lenticular valves in the older formations and in the younger growth stages, but in mature and old forms with the dorsal valve usually larger than the ventral. Surface ornamented by costellæ, often hollow. In the

¹⁰⁸ *Pionodema*, earliest of the Schizophoriidæ, appears simultaneously with the Dalmanellidæ. It is therefore difficult at present to state with assurance what stock gave rise to *Schizophoria* and allies.

aberrant *Enteletinæ* this ornamentation is superimposed over broad undulations or plicæ. Shell fibrous, punctate.

The ventral interior is especially marked by prominent diductor scars, separated by a median ridge which becomes more and more elevated in the more advanced and geologically more recent genera. The dorsal cardinalia consist of tusklike brachiophores having widely divergent supporting plates; the cardinal process is typically dalmanelloid; the dorsal adductor scars are separated by an oblique ridge in the later forms. The cardinalia, being alike throughout the family, are its most significant feature. The dorsal pallial sinuses consist usually of three pairs; the two inner ones, given off at the anterior ends of the anterior adductor scars, bifurcate immediately at their inception and ex-

Table 13



tend to the front margin as four subparallel trunks. The third pair is given off from the oblique ridge separating the adductor scars and extends to the front margin nearly parallel to the other sinuses. The inner four trunks are usually the more prominent.

GEOLOGIC RANGE.—Ordovician (Chazy) to Permian.

The Schizophoriidæ are subdivided into the following subfamilies:

- Schizophoriinæ Schuchert
- Enteletinæ Waagen
- Isorthinæ Schuchert and Cooper

The genetic relations appear to be as shown in Table 13.

DISCUSSION.—The Schizophoriidæ is one of the most easily recognized and longest lived families of the Dalmanellacea. It has its inception in the early Middle Ordovician (Chazy) with *Pionodema* as the oldest representative of the family, starting with the biconvex or lenticular shell phase. The passage from *Pionodema* to *Schizophoria* appears to be almost imperceptible. In *Pionodema* the ventral septum is low and long, being of the euseptoid type (Fredericks), and is the place of attachment of the adductor muscles. This septum increases in height during geological time and attains its final development in *Orthotichia* and

Enteletes. In *Pionodema* the adductor scars are clearly visible on the median ridge, and although in the geologically higher forms no adductor scars are visible on the floor of the valve, the presumption is that they were also borne on the septum.

The cardinalia are nearly uniform throughout the Schizophoriidæ from *Pionodema* to the last of the *Enteletes* in the Permian. The brachiophores are always shaped like the tusk of a boar, sharp and curved. The supporting plates are widely divergent and always have a small fulcral plate defining the socket. The cardinalia are perhaps the most distinctive structures in the whole group and their uniformity from genus to genus throughout the range of the family is a rather definite expression of the value of the cardinalia as a family characteristic.

The modification of the dorsal musculature from *Pionodema* to *Orthotichia* has some value in chronological stratigraphy. In *Pionodema* the adductor scars have a quadripartite arrangement, the posterior scars directly in back of the anterior pair and separated by horizontal ridges. Later, however, in Devonian and Mississippian times, the posterior adductors have migrated laterally and taken a position outside of and posterior to the anterior pair. These scars, further, are rather oval in outline instead of subcircular or quadrate as in the earlier forms, and are separated by an oblique ridge. The two oval scars one above the other produce a subflabellate appearance much like that of the ventral valve of *Rhipidomella*. The lateral migration of the posterior scars leaves a large central area occupied only by the much reduced median septum. The higher, more specialized forms such as *Orthotichia*, *Enteletes*, *Parenteletes*, etc., continue the dorsal musculature of the later Schizophorias.

Subfamily SCHIZOPHORIINÆ Schuchert 1929

Lenticular, or convexo-concave Schizophoriidæ not having numerous strong undulations or plicæ developed at the front end of the shell.

GEOLOGIC RANGE.—Middle Ordovician (Chazy) to Permian.

Embraces the following genera:

- Pionodema* Foerster
- Schizophoria* King
- Orthotichia* Hall and Clarke
- Aulacophoria* Schuchert and Cooper

The genetic relations are thought to be as shown in Table 14.

In this subfamily we place *Pionodema* as the originating stock of the Schizophoriidæ, this genus giving rise to *Schizophoria* out of which came the culminating *Orthotichia*. *Pionodema* and *Schizophoria* form interesting homœomorphs with *Schizophorella* and

Hebertella of the Plectorthinae. *Schizophorella* is the lenticular type of hebertelloid evolution, just as *Pionodema* represents the same phase in the development of *Schizophoria*. The convexo-concave profile of *Hebertella* corresponds to the similar shell form in *Schizophoria*.

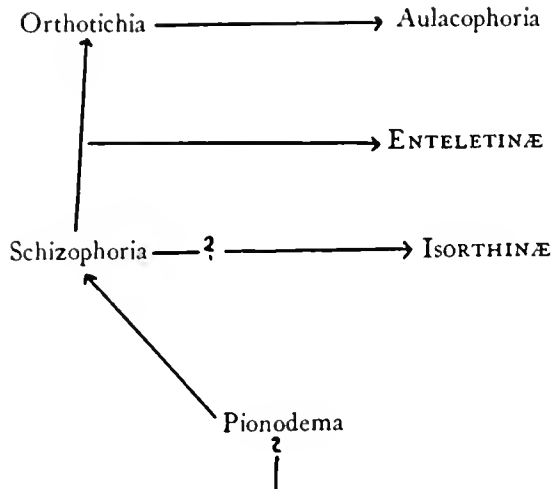
Genus PIONODEMA Foerste 1912

Pl. 23, figs. 1-10, 12-14; pl. 29, fig. 1

Foerste, Bull. Denison Univ., vol. 17, 1912, p. 139.
Cooper, Jour. Pal., vol. 4, 1930, pp. 369-382.
Hom. *Bathycælia* Foerste 1909.

GENOHOLOTYPE.—*Orthis subæquata* Conrad 1843, Proc. Acad. Nat. Sci. Phila., vol. 1, p. 333; Cooper, op. cit., pl. 35, fig. 4, pl. 36, figs. 1, 3, pl. 37, fig. 6.

Table 14



DESCRIPTION. *Exterior.*—Semi-oval or subglobose, margins convex, cardinal extremities obtuse, hinge-line slightly narrower than the greatest width of the shell, lateral profile lenticular or globose, the anterior part of the ventral valve becoming concave at the front; anterior commissure unisulcate or uniplicate; ventral interarea longer than the dorsal, gently curved, apsacline, beak slightly incurved, umbo prominent; dorsal interarea curved, orthocline, umbo convex, sulcate; delthyria open or partially closed by an apical plate; multicostellate, with hollow costellæ; shell fibrous, punctate.

Ventral interior.—Delthyrial cavity deep; teeth small, triangular; crural fossettes oblique; dental plates sharply defined, widely divergent, continued forward as a slight ridge of adventitious shell for a short distance along the lateral margin of the muscle area;

muscle area not confined to the delthyrial cavity, longer than wide; diductor scars divergent, subsemi-flabellate; adductor impressions consisting of two elongate semielliptical scars on a small ridge between the diductors; adjustor scars elongate, situated at the base of the dental plates. Apex closed by a small apical plate, the front of which is bevelled slightly below the level of the interarea. This plate clearly served for the attachment of the pedicle. Ovarian impressions occupy the umbo-lateral spaces.

Dorsal interior.—Cardinalia confined; brachiophore supporting plates not separable, vertical or nearly so, divergent at their bases; brachiophores sharp, divergent, shaped like a boar's tusk; sockets small, excavated beneath the palintrope, defined by a small concave fulcral plate which also serves to bind the brachial apparatus to the wall of the valve; cardinal process very small, expanded and bilobed posteriorly, its shaft being extended forward to merge with the low median ridge that extends forward nearly to the middle of the shell. Muscle area very faintly impressed, anterior adductor scars the larger.

GEOLOGIC RANGE.—Early Middle Ordovician (Chazy) to Upper Ordovician (Maysville).

AMERICAN SPECIES

Dalmanella bellula (Meek) 1873
D. circularis (Winchell) 1880
D. conradi (Winchell) 1880
D. subæquata (Conrad) 1843
Pionodema minnesotensis Cooper (Jour. Pal., vol. 4, 1930, pp. 374, 379, pl. 36, fig. 14)
P. uniplicata Cooper (Ibid., pp. 374, 379, pl. 35, figs. 1, 2)

EUROPEAN SPECIES

Orthis redux Barrande 1847

DISTINGUISHING CHARACTERS.—The diagnostic characters of *Pionodema* are the globose lateral profile, long ventral interarea, ventral musculature, and especially the structure of the cardinalia, which is most like that in *Schizophoria*, *Orthotichia*, and *Enteleles*.

DISCUSSION.—Foerste separated this group in 1909 under the name *Bathycælia* but later changed it to *Pionodema* when he learned that the former name was preoccupied. There was no description of the genus, the author merely stating that *Dalmanella subæquata* typified the group and that it ranged from the Stones River to the Devonian. It was unfortunate that the genus was so loosely defined, as it now makes great difficulty in the correct interpretation of the genotype. It has been shown in the discussion of *Doleroides* (p. 63) how shells of external character nearly identical to that of *P. subæquata* actually differ very markedly internally and can not be referred even to the same family. It becomes necessary, therefore, to give an analysis of the type of *Orthis subæquata* and from this to build a proper definition of the genus.

The types of *O. subæquata* are preserved in the American Museum of Natural History, catalogue number 910. There are four specimens in the lot, one of them considerably injured and too imperfect to be of any value in this discussion. Another is an internal mold of a small specimen which proves to be a *Doleroides*, probably *D. pærvetus*, since the ventral side of the specimen has a very marked sulcus. The third specimen is a silicified free ventral valve, undoubtedly of the same species as the fourth specimen, which is the shell figured by Hall as Conrad's type of *O. subæquata*.¹⁰⁹ Unfortunately, the latter is also a silicified specimen, so that it is quite impossible to determine the microstructure of the shell; it is small, 16.5 mm. wide, 14.5 mm. long, and 9 mm. thick. The following remarks will supplement Hall's description.¹¹⁰ In the dorsal valve there is a median sulcus which extends for about one-half the length of the valve, after which it is lost and the surface of the shell toward the anterior margin is quite regular, making for a nearly rectimarginate anterior commissure. However, a rather poorly defined fold on the ventral valve extends to the anterior margin and there produces a slight ventral undulation of the commissure. Swollen, hollow ribs are prominent on the surface of the shell. There is absolutely no single characteristic which will serve to set this shell apart from its numerous closely similar associates from the same locality. The ventral interior referred to previously is that of a small shell which is strongly but evenly convex. The dental plates are nearly obsolete but are continued forward as a low ridge nearly to the anterior ends of the diductor scars. The adductors are not enclosed by the diductors, which are elongate. The adjustors are situated at the base of the dental plates. This musculature is of the same type as that seen in punctate shells having the same external appearance as the type of *O. subæquata*. Hall and Clarke¹¹¹ referred *O. subæquata* to *Dalmanella* s. l., and in so doing admitted it to the punctate division of the orthids. They also refer to this species as a punctate shell on page 194. Winchell and Schuchert¹¹² likewise stated that *O. subæquata* is punctate but made no reference to the shell structure of any of the other forms associated with it. Foerste made no allusion to shell structure or any other important anatomical features. His reference to *Pionodema* as a subgenus of *Dalmanella* does imply, however, that he considered the group to be punctate. Therefore the name *Pionodema* is here used for punctate shells having an internal structure as described above. The use of the name thus is justi-

fied on the basis of the close similarity of the punctate shells referred to *D. subæquata* by Hall and Clarke and Winchell and Schuchert, and the close similarity of structure of the ventral interior (paratype) referred to above with ventral interiors of shells known to be punctate.

The ventral musculature of *Pionodema* is quite variable according to the development of the adjustor scars, which widen the field, and according to the length and width of the median ridge which bears the adductors. Frequently the adductor ridge is produced forward nearly to the anterior margin. In the dorsal valve the chief variation is in the angle of divergence of the crural apparatus and the presence or absence of the curved ridges of adventitious shell that extend forward from the brachiphore supports to unite with the median ridge. Externally there is considerable variation, especially in the degree of development of the fold and sulcus.

Pionodema finds its closest relatives in *Schizophoria* of Silurian and later strata, and it may be looked upon as the progenitor of this group. The external resemblance is no less striking than that of the interior. Indeed, Schuchert in Zittel¹¹³ states that *Pionodemas* "resemble small *Schizophoria* but are impunctate." As shown above, however, *Pionodema* as now restricted is actually punctate and therefore falls easily and naturally into the *Schizophoria* line. Internally there is the adductor ridge which becomes more prominent in *Schizophoria*, and the dorsal valve possesses crural apparatus that is identical in its essentials to that of *Schizophoria*.

For the progenitor of *Pionodema*, search must be made in the Chazy. Hall and Clarke state¹¹⁴ that *Dalmanella* had its "inception in the Chazy fauna" with *O. subæquata*. This is, however, probably an error, as all of the northern Chazy *Pionodemas* known to us are impunctate and internally ally themselves with *Doleroides* or *Mimella*. True *Pionodema* occurs in the Stones River and this pushes the *Pionodema* ancestor to pre-Stones River time. This ancestor is therefore unknown. It may have evolved from some impunctate stock, but it seems more likely that it came out of some group in which punctuation had already been established.

Pionodema appears to be confined mostly to American strata. Raymond¹¹⁵ has referred to this genus *Orthis girvanensis* Davidson (emend. Reed), but without a knowledge of the interior. In the Bohemian fauna, *Orthis redux* Barrande has internal characters that are very similar to those of *Pionodema* and comes from a corresponding horizon (Black River) (see pl. 23, figs. 2, 4).

¹⁰⁹ Pal. N. Y., vol. 1, 1847, pl. 32, fig. 2.

¹¹⁰ Ibid., p. 118. In studying Hall's description the reader must bear in mind that his use of the terms dorsal and ventral valve is the exact reverse of the current usage.

¹¹¹ Pal. N. Y., vol. 8, pt. 1, 1892, p. 207.

¹¹² Minnesota Geol. Surv., vol. 3, 1895, p. 447.

¹¹³ Zittel-Eastman Text-book of Paleontology, 2d ed., vol. 1, 1913, p. 382.

¹¹⁴ Op. cit., p. 207.

¹¹⁵ Bull. Mus. Comp. Zool., vol. 68, no. 6, 1928, p. 308.

Genus **SCHIZOPHORIA** King 1850

Pl. 23, figs. 11, 16-18, 20-25; t. fig. 12

King, Mon. Perm. Foss., 1850, pp. 105, 106.

GENOHOLOTYPE.—*Conchylolithus Anomites resupinatus* Martin 1809, Petref. Derb., pl. 49, figs. 13, 14.

DESCRIPTION. *Exterior.*—Externally like *Hebertella*; margins rounded, cardinal extremities rounded, hinge-line usually narrower than the greatest width of the shell; lateral profile resupinate, convexity of valves varying, the dorsal valve always with the greater convexity; anterior commissure rectimarginate to uniplicate; dorsal valve frequently with a low fold; ventral valve frequently sulcate in front; ventral palintrope the longer, faintly or strongly apsacline, curved or plane, beak slightly or strongly incurved, umbogently or strongly convex; dorsal palintrope short, curved, very strongly apsacline so that it overhangs the ventral interarea; multicostellate, with abundant hollow costellæ; test fibrous, punctate.

Ventral interior.—Delthyrial cavity usually deep; teeth strong; crural fossettes oblique; dental plates strong, frequently obscured by adventitious deposit, extended about the margins of the muscle area as a low ridge; muscle area bilobate or obcordate; diductor scars long, divergent, separated by a wide or narrow ridge having its origin a short distance forward of the apex; adductors small, borne on the median ridge; adjustor impressions usually long and tenuous, situated on the outside margins of the diductors.

Dorsal interior.—Cardinalia large; brachiophores scarcely separable from their supporting plates, vertical, or nearly so, strongly divergent, continued forward slightly as a ridge along the lateral margins of the muscle field; cardinal process in young shells like that of *Rhipidomella*, but in old shells largely resorbed, making a narrow ridge. In old shells an elevation is frequently formed on each side of the cardinal process in the notothyrial cavity. Muscle area quadripartite, the anterior pair of diductors being separated from the posterior pair by oblique ridges extending antero-laterally from the median ridge; peripheral margins thickened and elevated in some species. Pallial sinuses prominent, six in number, four of these taking their origin at the anterior extremity of the median ridge, starting as two trunks, then dividing into four and extending anteriorly in a subparallel arrangement, repeatedly branching near the anterior margin into subsidiary rami. Two other trunks originate, in some species, at the end of the ridge dividing the adductors, passing antero-laterally, bifurcating near the margin and then becoming arborescent at the margin.

GEOLOGIC RANGE.—Silurian (Clinton) to Pennsylvanian, with a very wide geographic distribution.

AMERICAN SPECIES

Schizophoria chouteauensis Weller 1914
S. cora (D'Orbigny) 1842
S. floydensis Belanski 1927
S. iowensis (Hall) 1858
S. iowensis magna Fenton and Fenton 1924
S. macfarlani (Meek) 1868
S. multistriata (Hall) 1857
S. oriskania Schuchert 1913
S. poststriatula Weller 1914
S. prima Stauffer 1918
S. resupinoides (Cox) 1857
S. sedaliensis Weller 1914
S. senecta Hall and Clarke 1892
S. striatula (Schlotheim) 1813
S. striatula marylandica Clarke and Swartz 1913
S. swallovi (Hall) 1858
S. tulliensis (Vanuxem) 1842
Rhipidomella subelliptica (White and Whitfield) 1862

FOREIGN SPECIES

Schizophoria beaumonti (Verneuil) 1849-1850
S. fragilis Kozłowski 1929
S. infracarbonica Janisevskij 1911
S. interstriata Janisevskij 1911
S. provulvaria (Maurer)
S. resupinata (Martin) 1809
S. resupinata lata Demanet 1921-1923
S. resupinata rotundata Demanet 1921-1923
S. striatula (Schlotheim) 1813
S. vulvaria (Schlotheim) 1820

DISTINGUISHING CHARACTERS.—*Schizophoria* is distinguished by its convexo-concave profile, the divergent or subparallel diductor scars in the ventral valve separated by a low median ridge (euseptoid) which bears the adductor marks, and in the dorsal valve by the widely divergent crural apparatus, characteristic muscle marks, and pallial trunks. The adductor muscles are separated by a curved, oblique ridge, a feature which at once separates this genus from *Proschizophoria*. The pallial marks consist of four or six subparallel trunks. *Schizophoria* closely resembles *Hebertella* externally, but the fundamental difference in shell structure and cardinalia serves to differentiate them immediately. The similarities and differences between *Orthotichia* and the genus under discussion are pointed out under the former genus.

DISCUSSION.—*Schizophoria* is a long-ranging genus and for this reason shows considerable variation in its internal anatomy. In the ventral valve the variation is seen in the musculature and the dental plates. The diductor scars vary from subparallel and extremely elongate in some species (*S. vulvaria* and *S. beaumonti*, Lower Devonian of Germany) to widely divergent and large or small (*S. propinqua*, *S. provulvaria*, and *S. multistriata*). In *S. iowensis* the muscle area is obcordate and much like that of *Hebertella*. Occasionally the adjustor scars are considerably developed,

with the result that the muscle area is notably expanded in front and is a trapezium in outline. The median ridge carrying the adductor scars varies from thin to very wide and in a few forms (*S. iowensis*, *S. striatula*) is extended forward beyond the anterior margin of the muscle area. In some specimens of *Schizophoria* from the Pennsylvanian the median ridge has attained the profile and height seen in *Orthotichia*. In the ventral valves of *S. resupinata*, there are two pallial sinuses extending forward from the anterior ends of the diductors and bowing outward in a considerable curve.

In the dorsal valve there are some notable variations in the musculature and pallial markings. In specimens of the genotype, *S. resupinata*, the arrangement of the adductor scars is nearly identical to that seen in *Orthotichia*, with the exception that the anterior scars are not in contact and that the space between the longitudinal sets is not so great as in the latter genus. In the early *Schizophorias* the muscle field is compact and the right and left sets of adductors are in close proximity, being separated only by a low median ridge, but in the later forms the longitudinal sets migrate laterally so that there is a notable space between them occupied only by a remnant of the formerly large median ridge. This lateral spreading of the two longitudinal sets of muscles reaches its maximum in *Orthotichia*. The generic difference between *Orthotichia* and *Schizophoria*, therefore, is certainly not very great.

The pallial markings are usually well developed, especially in the dorsal valve; *S. macfarlanei* shows the common type. This species has four parallel trunks extending anteriorly from the front margin of the anterior adductors to the shell margin, scarcely branching during their passage. Rarely there are six of these trunks, the two outside ones corresponding to the lateral trunks of *Isorthis*. So deep are these sinuses in *S. macfarlanei* that they have impressed themselves deeply in the shell, so that the slightest exfoliation of the shell laminæ shows these sinuses as ridges. The so-called *S. propinqua* (Hall) has pallial markings of the *Isorthis* type and has accordingly been placed with that genus.

The earliest undoubted *Schizophoria* is *S. senecta* from the Clinton of New York and probably also from Port Daniel, Quebec. Therefore the group must have its inception in the Ordovician, in *Pionodema*, whose external resemblance to *Schizophoria* has already been remarked upon. Furthermore, in the ventral valve of *Pionodema* there is an incipient adductor ridge and the structure of the cardinalia in the dorsal valve is identical in every fundamental detail with that of *Schizophoria*.

Genus ORTHOTICHIA Hall and Clarke 1892

Pl. 24, figs. 12, 15, 22-24, 27

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, p. 213, pl. 7, figs. 11-15.

GENOHOLOTYPE. — *Orthis* ? *morganiana* Derby 1874, Bull. Cornell Univ., vol. 1, p. 29, pl. 3, figs. 1-9, 11, 34, pl. 4, figs. 6, 14, 15.

DESCRIPTION. *Exterior*.—Externally like *Schizophoria* but usually more finely ornamented.

Ventral interior.—Umbonal cavity deep; teeth strong; dental plates strong, divergent, extended nearly to the middle of the valve as high septal ridges about the lateral margins of the muscle area; the cavity defined by these plates is centrally divided by a median septum, which takes its origin a short distance in front of the apex, rising to its maximum height a little in front of the ends of the dental plates, where it is abruptly truncated. Diductor and adjustor scars confined to the areas between the dental plates and the median septum; adductor scars attached to the sides of the median septum.

Dorsal interior.—Cardinalia strong; brachiophores strong, tusklike, supported by strong plates that diverge around the lateral margins of the muscular area; all of these structures are intimately fused together; the sockets are deep and are defined by a thin concave fulcral plate which unites the crural apparatus to the palintrope. Cardinal process small, "multifid"; muscle area quadripartite, the anterior adductors subtriangular or irregularly oval, situated so that their antero-median extremities are in contact, the posterior extremities being divergent and separated by the expanded extremity of the low median ridge; the anterior adductor scars on the outside of and slightly posterior to the anterior pair and separated from them by a narrow, curved, oblique ridge. Anterior scars narrow subparallel grooves separated by a low ridge. Pallial markings as in *Schizophoria*.

GEOLOGIC RANGE. — Pennsylvanian to Permian. Distribution world wide.

AMERICAN SPECIES

Orthotichia morganiana (Derby) 1874

O. schuchertensis Girty 1903

O. kozlowskii King 1930 (= 1931)

? *O. texana* Girty 1928

FOREIGN SPECIES

Orthotichia chekiangensis Chao 1927

O. frechi Fliegel

O. indica (Waagen) 1884

O. marmorea (Waagen) 1884

O. morganiana (Derby) 1874

O. morganiana chihsiensis Chao 1927

DISTINGUISHING CHARACTERS.—*Orthotichia* is distinguished by the presence of three strong septal plates in the ventral valve, the outer two being the divergent dental plates; the inner or median ridge rises to a crest at the front of the muscle area as in *Enteletes* and is obliquely truncated. This genus most closely resembles

certain forms of Mississippian and Pennsylvanian *Schizophoria* but differs from them in the degree of development of these plates. In *Orthotichia* the dental plates are always high and extend to the front of the muscle area as high ridges. Some Pennsylvanian species of *Schizophoria* approach *Orthotichia* in the accelerated development of the median septum but in them the dental plates have not attained the specialized character of those in *Orthotichia*.

DISCUSSION.—The dorsal valve has the general characteristics of the Pennsylvanian *Schizophoria*. The posterior adductor scars are situated behind and outside of the anterior impressions, being separated by a low oblique ridge that is antero-laterally directed. The individual scars are rather elongate, tapering posteriorly but expanded toward the front. This gives the muscle-scars a flabellate outline where viewed in the aggregate. It was Derby's idea¹¹⁶ that there were six adductor impressions in the dorsal valve. The smooth spaces on each side of the low median ridge were interpreted as muscle-scars but there is no crenulation or any other sign of muscle attachment in the three spaces. Hall and Clarke¹¹⁷ also suggested a third pair of dorsal muscles in *Schizophoria macfarlandi*. The specimen to which they refer is an old obese shell in the Schuchert Collection. What appear to be lateral muscles are actually pits left by the incomplete covering up of the brachioophore apparatus by adventitious shell.

Orthotichia structurally forms the passage between *Schizophoria* and *Enteleles* but this does not necessarily mean that the latter actually developed out of *Orthotichia*. *Enteleles* probably developed directly out of the more plastic *Schizophoria*, and *Orthotichia* may then be a terminal branch of the *Schizophoria* line.

Genus AULACOPHORIA Schuchert and Cooper 1931

(Gr. *aulax*, furrow; *phorecin*, to bear)

Pl. 29, figs. 2, 5, 10

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 247.

GENOHOLOTYPE.—*Orthis keyserlingiana* De Koninck 1843, Desc. Anim. Foss. Terr. Carb. Belgique, p. 230, pl. 13, fig. 12.

DESCRIPTION.—*Aulacophoria* is proposed for shells having an interior like that of *Schizophoria* but having a deep sulcus on the dorsal valve and a strong fold on the ventral one. Besides the genotype, two other European species are placed in this genus, *Enteleles infracarbonica* Janisevskij from the Lower Carboniferous of the eastern Urals in the vicinity of Khabarny

and *E. uralica* Gorsky from the Middle Carboniferous of the eastern slope of the Urals. *Schizophoria* (*Enteleles*?) *mesoloba* Janisevskij may be another form belonging in this genus.

In the dorsal valve the brachioophore plates are widely divergent as in *Schizophoria* and *Enteleles*, and the sockets are defined by fulcral plates as is usual in the family. In the ventral valve the prominent dental lamellæ are subparallel but no prominent median septum was detected, such as occurs in *Orthotichia* or in *Enteleles*. The ornamentation is very much like that of *Enteleles*, much more so than like *Schizophoria*.

Aulacophoria thus occupies an intermediate position structurally between *Enteleles* and *Schizophoria*. It differs from the former in being less ventricose and inflated and in not possessing the prominent ventral median septum. The great development of the median septum in *Enteleles*, according to Gorsky, may be an adaptation to the great inflation of the valves to accommodate the attachment of the adductor or closing muscles.

Gorsky¹¹⁸ maintains that the type of structure shown by *Enteleles infracarbonica* Jan. represents the earliest phase of *Enteleles*. It is our idea, on the other hand, that *Aulacophoria* is a terminal offshoot from *Schizophoria*. We base this conclusion on the greater resemblance of the interior to *Schizophoria* than to *Enteleles*.

Subfamily ENTELETINÆ Waagen 1884

Aberrant, globular or strongly biconvex Schizophoriidæ that are usually strongly plicate in front, or atavistically ? smooth.

GEOLOGIC RANGE.—Pennsylvanian and Permian. Embraces the following genera:

Enteleles Fischer de Waldheim
Enteletina Schuchert and Cooper
Parenteleles King
Enteletella Likharev
Enteletoides Stuckenberg

The genetic relations seem to be as shown in Table 15.

DISCUSSION.—The Enteletinæ in their comparatively short life span have tried to adopt several of the features developed in other groups by more tedious routes of evolution. *Parenteleles* tried the cella or camera of *Merista*. *Enteletella* developed a spondylium for muscle attachment. Further, there was no stability in the development of the fold and sulcus. This trait is not unusual among the orthids but in the Enteletinæ a ventral fold became persistent in two

¹¹⁶ Bull. Cornell Univ., vol. 1, 1874, p. 30.

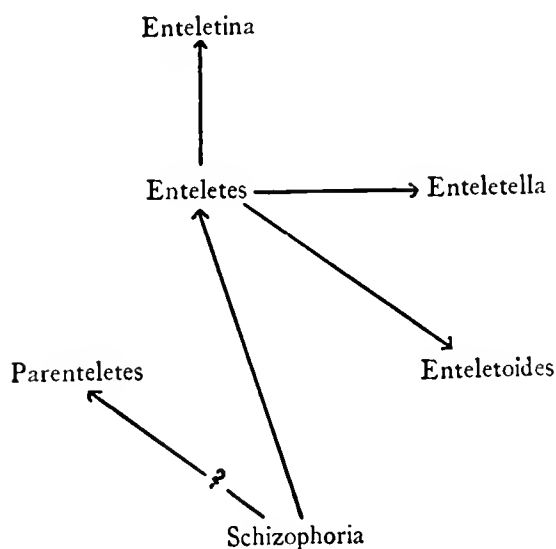
¹¹⁷ Pal. N. Y., vol. 8, pt. 1, p. 214.

¹¹⁸ Bull. Com. Géol. Leningrad, vol. 43, no. 9, 1927, pp. 1184-1186, pl. 18, fig. 9.

stocks and therefore of use in the definition of two genera along with other features.

The evolution of the *Enteletinae* is somewhat analogous to that of the *Derbyias* and *Meekellas* which lived at about the same time. In the last named genus the shell also develops broad undulations at the front as in *Enteletes*. It would be interesting to know what conditions of ecology in the Pennsylvanian and Permian seas could have produced such parallel developments in these two different stocks. Or is it an expression of old age in these terminal stocks that arose so far back in the Ordovician?

Table 15



Genus ENTELETES Fischer de Waldheim 1825

Pl. 24, figs. 1-3, 5-10, 25

Fischer de Waldheim, Notice sur la Choristite, 1825, p. 6; Oryct. Gouv. Moscou, 1830-1837, p. 144, pl. 24, figs. 10-11 (*choristites* = *lamarcki*), pl. 26, figs. 6-7 (*glaber*).

GENOHOLOTYPE.—*E. choristites* Fischer de Waldheim 1825 = *Spirifer lamarcki*.

DESCRIPTION. *Exterior*.—More or less globular, margins convex; hinge-line narrower than the greatest width of the shell; cardinal extremities rounded; lateral profile unequally biconvex, the dorsal valve being the more convex; lateral commissure dorsally deflected near the hinge; anterior commissure uniplicate; ventral interarea the longer, curved, apsacline, beak strongly incurved, umbo swollen; dorsal interarea short, curved, orthocline to apsacline, beak strongly incurved, umbo tumid; delthyrium open,

notothyrium partially closed by the cardinal process. Surface finely costellate, and plicate anteriorly. Shell fibrous, punctate.

Ventral interior.—Umbonal cavity deep; teeth strong; crural fossettes oblique; dental plates strongly developed, advancing, slightly convergent or subparallel; the space between these plates divided medianly by a thin bladelike septum rising to an apex at its anterior extremity, truncated sharply in front so that it terminates in a line with the anterior termination of the dental plates; muscle area compressed laterally; diductors and adjustors confined to the narrow areas between the dental plates and the septum, while the adductors were probably attached to the latter.

Dorsal interior.—Cardinalia strong; brachioophores strong, curved, supported by thin plates that are extended forward and around the lateral margins of the muscle area as far as the anterior margin. Sockets strong, defined by a socket-plate on the outside margin of the socket; along the hinge-line a strong denticle; cardinal process small; muscle area like that of *Orthotichia*, the anterior adductor scars large, subcircular; the posterior adductors forming two small scars on the outside of and slightly posterior to the anterior adductors and next the ridges from the brachioophore supports.

GEOLOGIC RANGE.—Middle Pennsylvanian to Permian in many parts of the world.

AMERICAN SPECIES

- Enteletes andii* (D'Orbigny) 1842
- E. dumblei* Girty 1908
- E. hemiplicata* (Hall) 1852
- E. leonardensis* King 1930 (= 1931)
- E. liumbonus* King 1930 (= 1931)
- E. plummeri* King 1930 (= 1931)
- E. wolfcampensis* King 1930 (= 1931)
- E. wordensis* King 1930 (= 1931)

FOREIGN SPECIES

- Enteletes contractus* Gemmellaro 1898
- E. elegans* Gemmellaro 1898
- E. haugi* Gemmellaro 1898
- E. hemiplicatus naia* Fredericks 1923
- E. kayseri* Waagen 1884
- E. laevissimus* Waagen 1884
- E. lamarcki* Fischer de Waldheim 1825
- E. meridionalis* Gemmellaro 1898
- E. microplocus* Gemmellaro 1898
- E. oehlerti* Gemmellaro 1898
- E. subaequivalvis* Gemmellaro 1898
- E. tschernyscheffi* Diener
- E. waageni* Gemmellaro 1898

? *E. pentamera* Eichwald

DISTINGUISHING CHARACTERS.—*Enteletes* is distinguished externally by its elliptical outline, globular profile, and plicate anterior. Internally the subparallel dental plates and sharp, crested median septum

are diagnostic characters. From *Orthotichia* it differs in the presence of the anterior plications and in the subparallelism of the dental plates. It differs from *Enteletina* and *Parenteles* in having the fold on the dorsal valve. *Enteletella* differs from this genus in the possession of a spondylium.

DISCUSSION.—Waagen¹¹⁹ proposed two groups of *Enteles*: (1) the "ventrisinuate" group having the fold on the dorsal valve; and (2) the "dorsosinuate" group which has the fold on the ventral valve. King¹²⁰ has recently separated the latter group as a new genus called *Parenteles*. The new generic group is, however, not homogeneous and should be further split into two groups on the basis of internal structure. The term *Enteles*, then, must be restricted to shells of the *E. lamarcki* and *E. hemiplicatus* type, which have the fold and sulcus in the usual position. Specimens having a small sulcus in the fold and a plication in the sulcus are not excluded from *Enteles*; this condition does not alter the uniplicate character of the anterior commissure and is not considered of sufficient import for the separation of a new group.

Waagen¹²¹ suggested that *Enteles* evolved from *Orthotichia* by the development of plicæ in the anterior part of the shell, and this idea has gained quite general acceptance. *Enteles* is the culmination of a long line of orthid evolution that began in Chazy time with *Pionodema*. It appears in the Middle Pennsylvanian and ranges through the Permian. By loss of the plicæ in late Permian time it is thought to have returned to the ancestral *Orthotichia*-like condition, this atavistic phase of *Enteles* being termed *Enteletoides* by Stuckenbergh.

It is thought by the writers that *Orthotichia*, which ranges from the Pennsylvanian to the Permian, is probably a terminal stock of the Schizophoriidæ and may not have given rise to *Enteles*. We suggest the separate development of *Enteles* out of *Schizophoria* in the Pennsylvanian at about the same time as the appearance of *Orthotichia*.

Gorsky¹²² has claimed the development of *Enteles* from *Orthotichia* by way of simply plicated stocks like *Aulacophoria*. We hold, rather, that *Aulacophoria* is a side line out of *Schizophoria*, and one that probably did not survive beyond the middle Pennsylvanian.

Genus PARENTELETES King 1931

Pl. 24, figs. 11, 13, 14, 16, 18, 21, 26

King, Bull. 3042, Univ. Texas, 1930 (1931), p. 48, pl. 1, figs. 16-20; pl. 2, figs. 1-3.

¹¹⁹ Mem. Geol. Surv. India, Pal. Indica, ser. XIII, vol. 1, pt. IV, fasc. 3, pp. 553-563.

¹²⁰ Bull. 3042, Univ. Texas, 1930 (1931), p. 48.

¹²¹ Op. cit., p. 564.

¹²² Op. cit., 1927.

GENOHOLOTYPE.—*P. cooperi* King 1931.

DESCRIPTION. *Exterior*.—Externally like *Enteles*, but somewhat more transverse, dorsosinuate; lateral profile unequally biconvex, the dorsal valve the larger; anterior commissure sulcate; ventral interarea the longer, apsacline, beak strongly incurved, umbo swollen, delthyrium large; dorsal interarea short, curved, apsacline, beak strongly incurved, umbo tumid, notothyrium wide. Surface multicostellate and plicate, rugose, with hollow costellæ, the plicæ broad and angular. Shell fibrous, punctate, the punctæ arranged in narrow radial rows.

Ventral interior.—Delthyrial cavity deep, teeth elongate, sockets pointed; dental plates strong, subparallel posteriorly but diverging strongly anteriorly; area between them divided by a median septum which originates very close to the apex, rounded on its dorsal extremity, rising as it progresses forward to reach its maximum height at the point where the anterior ends of the dental plates die out. Here it is abruptly truncated and its extremity forms the crest of a V-shaped camera or cella, formed at the point where the internal sulcus corresponding to the fold has its origin. Musculature as in *Enteles*. A small plate for pedicle attachment is in the apex.

Dorsal interior.—Cardinalia and musculature like those of *Enteles*.

GEOLOGIC RANGE.—Upper Pennsylvanian and Lower Permian of Europe and America.

AMERICAN SPECIES

Parenteles cooperi King 1931

FOREIGN SPECIES

Enteles dieneri Schellwien 1900

E. suessi Schellwien 1892

E. suessi acuticosta Schellwien 1892

DISTINGUISHING CHARACTERS.—*Parenteles* differs from *Enteles* in having the fold on the ventral valve, and in the possession of a V-shaped camera or cella under the anterior portion of the median septum. This internal character also serves to differentiate the genus from *Enteletina*, which closely resembles it externally.

King has shown that *Parenteles* in America appears in geological time before *Enteles*, and this appears to indicate that the genus under discussion evolved separately from *Orthotichia* or *Schizophoria* and is not a modification of *Enteles*. Girty¹²³ and Waagen¹²⁴ have suggested that *Parenteles* (the dorsosinuate group) developed out of an *Enteles* having

¹²³ U. S. Geol. Surv., Prof. Paper 58, 1908, p. 290.

¹²⁴ Mem. Geol. Surv. India, Pal. Indica, ser. XVIII, vol. 1, 1887, p. 562.

a small sinus in the dorsal fold and a plication in the sulcus, by enlargement of said plication. While this is possible, the fact remains that *Parenteletes* was developed earliest. Furthermore, there is much more similarity between *Orthotichia* and *Parenteletes* in the divergence of the dental plates. Therefore the evidence points to an independent development of the two genera out of *Orthotichia*.

E. suessi, figured by Schellwien,¹²⁵ we place in association with American species of *Parenteletes*, as it shows, according to his figure, the same internal characteristics as the American forms. Schellwien remarked on the external similarity between *E. suessi* and the Indian *E. latesinuatus* Waagen, but pointed out the internal differences and on this basis separated the two species; his figure shows the walls of the camera uniting with the dental plates, but in American forms these are discrete. There is a possibility that the figure has not been drawn accurately.

The camera of *Parenteletes* is a remarkable convergence toward the type of muscle platform in *Merista*, *Dayia*, and *Cyclospira*, although the one in *Parenteletes* differs in bearing a median septum on its crest.

Genus ENTELETINA Schuchert and Cooper 1931

Pl. 24, figs. 17, 19, 20

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 247.

GENOHOLOTYPE.—*Enteletes latesinuatus* Waagen 1884, Mem. Geol. Surv. India, Pal. Indica, ser. XIII, vol. 1, pt. IV, fasc. 3, pp. 559-560, pl. 57, figs. 4-6.

DESCRIPTION. *Exterior*.—Externally *Enteletina* is identical with *Parenteletes* but internally it has all of the features of *Enteletes*. It therefore is essentially an *Enteletes* with the fold on the ventral valve and comprises Waagen's division of "dorsosinuates." The dental plates are not strongly divergent and there is a crested median septum which does not have the peculiar V-shaped camera so characteristic of *Parenteletes*. The presence of this chamber, the function of which is not understood unless it be for muscle attachment, is therefore not a distinction between the Asiatic and American and European "dorsosinuate" *Enteletes*.

The writers have selected Waagen's species *E. latesinuatus* to serve as the genotype, as both internal and external characters of it have been admirably figured. The Indian forms are all Upper Permian in age and may represent a development from *Enteletes* by the enlargement of plicæ in the ventral sulcus, such as suggested by Waagen and Girty. (See under discussion of *Parenteletes*.) We have placed in this genus only

the Late Permian species of India, and do not include here such Pennsylvanian and Lower Permian forms as *E. suessi* and variety *acuticosta* and *E. dieneri*, since their internal structure is clearly that of *Parenteletes*.

Enteletes globosus Girty, probably from the Word of late Middle Permian age, is placed here provisionally since its internal structure is not known.

GEOLOGIC RANGE.—Permian of India and Texas.

INDIAN SPECIES

Enteletes acutiplicatus Waagen 1884

E. ferruginea Waagen 1884

E. latesinuatus Waagen 1884

E. pentameroides Waagen 1884

E. sublaevis Waagen 1884

AMERICAN SPECIES

? *Enteletes globosus* Girty 1908

Genus ENTELETELLA Likharev 1924

Pl. 24, fig. 4

Likharev, Bull. Com. Géol., Leningrad, vol. 43, no. 6, 1924, pp. 719, 721, pl. 5, figs. 1-3.

GENOHOLOTYPE.—*E. nikschitschi* Likharev 1924.

DESCRIPTION.—*Enteletella* has the external form and ornamentation of a ventrisinuate or true *Enteletes*, closely resembling *E. microplocus* Gemmellaro. It differs internally from *Enteletes*, however, in the possession of a spondylium. The dental plates unite with the median septum in such a way as to enclose a portion of it, which projects as a ridge for the attachment of the adductors inside the spondylium. The dorsal edge of this ridge is somewhat club-shaped, and the lower part of the median septum remains free. The dorsal valve is, in all respects, the same as that of *Enteletes*. The genotype is the only species known.

GEOLOGIC RANGE.—Lower Permian of northern Caucasia.

Genus ENTELETOIDES Stuckenberg 1905

Stuckenberg, Mém. Com. Géol., n. ser., livr. 23, 1905, pp. 59, 129, pl. 6, fig. 8, pl. 9, fig. 8.

Gorsky, Bull. Com. Géol., vol. 43, no. 9, 1927, pp. 1184-1186, pl. 18, fig. 7 (*subrossicus*).

GENOHOLOTYPE.—*E. rossicus* Stuckenberg 1905.

DISTINGUISHING CHARACTERS.—Stuckenberg proposed this name for shells having a convexo-concave profile and multicostellate external ornamentation, recalling *Orthotichia* in both of these characteristics. According to that author the shell completely lacks interareas. Internally the arrangement of the dental plates and median septum is identical with that of

¹²⁵ Abh. k. k. geol. Reichsanst., Bd. 16, Heft 1, 1900, p. 12, pl. 1, fig. 18.

Enteleles. In other words, this is essentially an *Enteleles* showing atavistic tendencies toward *Orthotichia* in the loss of the radial plications and globose profile.

DISCUSSION.—The absence of interareas, while not impossible, is not convincing from the figures presented by Stuckenberg, especially figure 8e of plate 6. Such an arrangement of the dental plates and their connection with the lateral margins of the shell as indicated suggests a wide hinge-line, and the latter presupposes a palintrope. The shells of *Orthotichia* and *Enteleles* are usually thin and very susceptible to crushing; this may be the reason for the apparent lack of interareas in Stuckenberg's specimens. Parallelism of the dental plates would be an important clue to determining the ancestry of this form, but the figures of the author are not specially convincing on this point (see his fig. 8b, pl. 9). It may be questioned whether an *Enteleles* that has atavistically lost its radial ornamentation would likewise lose its most characteristic internal features and the globose contour of the shell as well.

Schellwien has made much of the supposition that many species now referred to *Orthotichia* may actually represent atavistic *Enteleles* and for this reason he referred all smooth forms having the internal structure of *Enteleles* to that genus, placing there even the genotype of *Orthotichia*. It is important, if it can be proved that atavistic forms of *Enteleles* actually exist, that these be separated under a new designation and not included in *Orthotichia*, which is essentially an incipient or potential *Enteleles*. It is also important to determine when these atavistic tendencies appear. They may have appeared soon after the origin of the genus, occurring several times during the Upper Pennsylvanian and Permian, or they may have been delayed till near the end of the Permian, in which case the matter is more simple. King (1931) maintains that the Permian *Enteleles*, in large part, are more strongly plicated than the Pennsylvanian species, and that the forms with faint plications do not even resemble *Orthotichia* in profile. If the atavism is actually carried to the degree of the resumption of the convexo-concave form of *Orthotichia*, the only reliable clue to the relationship of atavistic shells would be in the parallelism of the septal plates of the ventral valve. The parallelism of the plates in *Enteleles* is frequently more apparent than real, and it is often difficult to evaluate the degree of divergence that does exist. It will thus be seen that it is extremely difficult to establish the fact of atavism in these shells. It seems to the writers that unless the atavistic tendencies are inaugurated in the nepionic stage of *Enteleles*, *Enteletoides* should have the globose outline and interior of the former genus. If the return of the previous characters takes place in the nepionic stage, all objections in regard to profile in internal characters noted above lose their force.

Another species referred here is *Enteletoides subrossicus* Gorsky 1927, from the Middle Carboniferous on Kamenka River, eastern Urals.

Subfamily ISORTHINÆ Schuchert and Cooper 1931

Divergent biconvex Schizophoriidæ, having the ventral musculature, cardinalia, and pallial markings of *Schizophoria*. The only known genus is *Isorthis* Kozłowski, probably derived out of early Silurian *Schizophoria*.

Genus ISORTHIS Kozłowski 1929

Pl. 21, figs. 17-28, 30-33; pl. 23, figs. 15, 19;
t. fig. 13

Kozłowski, Pal. Polonica, vol. 1, 1929, pp. 29, 75, pl. 2, figs. 24-41, t. figs. 16-18.

GENOHOLOTYPE.—*Dalmanella* (*Isorthis*) *szajnochai* Kozłowski 1929.

DESCRIPTION. *Exterior.*—Transversely subelliptical, hinge-line straight, narrower than the greatest width of the shell; cardinal extremities rounded. Lateral profile unequally to subequally biconvex; anterior commissure rectimarginate to faintly sulcate. Dorsal sulcus shallow. Ventral palintrope longer than the dorsal, curved, gently apsacline. Beak curved, umbo swollen; delthyrium open. Dorsal palintrope short, faintly apsacline or faintly anacline; notothyrium closed by the cardinal process. Ornamentation multicostellate. Shell fibrous, punctate.

Ventral interior.—Delthyrial cavity deep; teeth large; crural fossettes deep; dental plates strong in young specimens, obsolete in old ones. Muscle field deeply impressed, bilobed in front; diductor scars elongate, subparallel; adductor track elevated, usually narrow, adductor scars semielliptical when visible; adductor scars located on the sides of the dental plates, usually not clearly visible. Pallial markings prominent, consisting of two main trunks extending antero-laterally from the anterior end of each diductor.

Dorsal interior.—Brachiophores as in *Schizophoria*, i. e., bladellike plates, with fulcral plates and usually supported by adventitious shell (see below). Cardinal process small, bilobed, trilobed, or multilobed, commonly modified by deposition of adventitious testaceous deposit. Median ridge low. Muscle area subcircular in outline, usually with thickened peripheries. Adductor scars subequal in size. Pallial sinuses consisting of three pairs of trunks as in *Schizophoria*; two originate at the antero-medial ends of the anterior adductor scars and extend anteriorly; a second set starts just outside the former and extends antero-laterally. The third

set appears at the line separating the anterior and posterior adductor sets, each trunk bifurcating into subsidiary ones (see discussion below).

GEOLOGIC RANGE.—Late Silurian (upper Ludlow) to Middle Devonian.

AMERICAN SPECIES

- Dalmanella arcuaria* Hall and Clarke 1892
D. perelegans (Hall) 1857
D. pygmæa Dunbar 1920
D. rockhousensis Dunbar 1920
Schizophoria propinqua (Hall) 1847

EUROPEAN SPECIES

- Dalmanella* (*I.*) *szajnochai* Kozłowski 1929
Orthis canalicula Schnur 1853 (1851?)
O. decipiens Barrande 1847
O. loveni Lindström
O. neglecta Barrande 1847
O. occlusa Barrande 1847
O. tetragona Roemer 1844
O. trigeri Verneuil

DISTINGUISHING CHARACTERS.—*Isorthis* is distinguished from *Dalmanella* by its strongly biconvex lateral profile, lack of prominent fold and sulcus, peculiar ventral and dorsal musculature, and brachiophores with fulcral plates.

DISCUSSION.—The ventral musculature with its elongate and divergent diductor impressions most strongly resembles that of certain species of *Schizophoria*. The diductor tracks are deep and elongate and are separated by a prominent ridge which carries the adductor muscles. A strong pallial trunk extends anteriorly from the ends of the diductor impressions. Branching of these primary trunks has not been observed.

In the dorsal valve the cardinal process is small, but, contrary to Kozłowski's statement, it has a lobate myophore, as shown by *I. canalicula* (Schnur) and other species placed in the genus. The pallial sinuses are well shown in *I. tetragona*, in which four trunks appear to originate at the antero-median extremities of the anterior adductor scars. In reality there are only two main trunks but they bifurcate almost at their origin and send out two secondary branches, one pair antero-medially, the other antero-laterally. A second pair of primary pallial sinuses is given off from the horizontal elevation dividing the adductor scars. This trunk bifurcates in about half the distance to the margin, sending one branch antero-laterally, the other postero-laterally. In makeup these sinuses are much like those of *Schizophoria*, as seen in *S. tulliensis* and *S. senecta*, in which all the trunks originate at the same place as in *Isorthis*, but since the shell ridge dividing the adductor scars is oblique they extend toward the front in a subparallel arrangement. *Schizophoria propinqua* (Hall) has pallial markings exactly like those of *Isorthis* and is therefore provisionally placed in that genus.

Of interest in *Isorthis* is the great development of adventitious shell deposited upon the cardinalia and in the vicinity of the dorsal muscular area. In some instances primary structures are nearly completely obscured.

Isorthis appears to be common in Europe, being well represented in the Lower Devonian of Bohemia and in the younger Eifelian of Germany. In America it is common in the Helderberg (New Scotland) (*I. perelegans*, *I. rockhousensis*, *I. pygmæa*), and in the Silurian of Tennessee it is represented by *I. arcuaria*.

Family LINOPORELLIDÆ Schuchert and Cooper 1931

Aberrant, specialized Dalmanellacea, having a dorsal cruralium and a shell ornamentation recalling *Porambonites*.

GEOLOGIC RANGE.—Silurian, with the genera *Linoporella* Schuchert and Cooper and *Orthotropia* Hall and Clarke.

DISCUSSION.—The ventral musculature of *Linoporella* is close to that of *Pionodema* and *Schizophoria*. In the dorsal valve, however, the convergence of the brachiophore plates to meet a median septum is such a radical departure from the usual structure of the Schizophoriidæ as to warrant the erection of a family to recognize this variation. The schizophorioid ventral muscles and the punctate shells indicate the probable origin of *Linoporella*, but the presence of a cruralium shows a distinct divergence from some stock as yet unknown, but probably to be looked for among the late Ordovician Schizophoriidæ.

Genus LINOPORELLA Schuchert and Cooper 1931

Pl. 18, figs. 13, 14, 17, 18, 24, 33

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 247.

GENOHOLOTYPE.—*Orthis punctata* Verneuil 1848, Bull. Soc. Géol. France (2), vol. 5, p. 343.

DESCRIPTION. *Exterior.*—Semioval to subglobose, margins convex; hinge-line narrower than the greatest width of the shell; cardinal extremities rounded; lateral profile subequally biconvex; anterior commissure slightly sulcate; ventral interarea the longer, curved, apsacline, beak strongly incurved, delthyrium open; dorsal interarea anacline, beak incurved; surface multicostellate, the striae being marked by a row of coarse pits which do not perforate the interior shell layer. Test fibrous, punctate.

Ventral interior.—Delthyrial cavity deep; teeth small, fossettes lacking; dental plates strong and

prominent, subparallel, produced forward as prominent ridges on each side of the diductor scars; a median ridge extends from the front of the muscle area nearly to the margin of the shell and is commonly extended between the diductor impressions nearly to the apex. Muscle field longer than wide; adductor scars borne on the median ridge; diductor scars elongate, narrow; muscle area thickened in front; irregular, wavy ovarian markings occupying the lateral spaces. The palintrope overhangs the delthyrial cavity.

Dorsal interior.—Cardinalia strong; notothyrial cavity deep; brachioophores forming a thickening below the notothyrial margin and terminating in short, blunt points supported by stout plates that converge to meet a median septum and thus make a cruralium; sockets shallow, excavated in the margin of the hinge and the outer face of the crural base, defined by an obscure fulcral plate; cardinal process unique, consisting of an elongate thickened myophore and a thin septum-like shaft that is continuous with the median septum. Median septum high, extended forward about half the length of the valve. Muscle area elongate-oval, divided by the median septum, commonly with an elevated periphery. Elevated, wavy visceral markings occupy the spaces outside of and posterior to the muscle area.

GEOLOGIC RANGE.—Middle Silurian or Gotlandian (Niagaran).

AMERICAN SPECIES

Orthis punctostriata Hall 1852

EUROPEAN SPECIES

Orthis punctata Verneuil 1848

? *O. turgida* McCoy 1851

DISTINGUISHING CHARACTERS.—*Linoporella* is unique among punctate orthoid genera in the convergence of its ornamentation toward the kind seen in *Porambonites*. There are, however, internal and external differences that when combined with the geological occurrences separate the two genera. Externally *Linoporella* has the outline and profile of *Pionodema*, differing thus from *Porambonites*, and internally the ventral musculature, dorsal cruralium, and cardinal process further serve to differentiate the two.

DISCUSSION.—Hall and Clarke (1892)¹²⁶ were aware of this group of orthids, saying of *O. punctata* and *O. punctostriata* that they could not be placed in their divisions of the old genus *Orthis*; they did not, however, give them a generic name.

The internal features of *Linoporella* separate the genus from all other Dalmanellacea. In the ventral valve of young shells the dental plates are sharply defined by deep umbonal cavities and extend directly

to the floor of the valve. In most specimens these plates are prolonged along the floor of the valve as low ridges. The diductor scars are semielliptical or semi-oval in plan and are separated by a depressed adductor ridge. The latter is low in the posterior of the shell but is elevated to a sharp crest at a point just in front of the anterior ends of the diductor scars, and then descends to disappearance near the front margin. Along the top of this ridge is a shallow, longitudinal groove which usually does not extend anterior to the crest. In older shells the front margins of the diductor scars are elevated on a low callus deposit which is elevated forward and inward along the median ridge and rises to disappearance at the crest. Posteriorly and laterally the callus decreases in thickness to become only a film on the sides of the dental plates and floor of the valve. This callus is significant, however, because it obscures the front ends of the dental plates and produces a pseudospondylium. Careful observation of old specimens will commonly show low extensions of the dental plates into or beyond the callus and its upturned anterior border. The delthyrial region of *Linoporella* is another significant example of obsolescence of primary structures (bases of dental plates in this instance) by secondary deposit of shell. In this tendency it also parallels *Porambonites*, although the degree to which the deposition is carried does not result in structures that are precisely alike.

The dorsal interior is also unique in *Linoporella*, being a convergence to that seen in *Skenidioides*. The brachioophores are elongate, toothlike, bluntly pointed processes extending into the interior of the valve. Their forward growth produces a thickening under the palintrope which lies on them and extends over the notothyrial cavity for a short distance. These processes merge into discrete convergent plates which unite near the floor of the valve with a sharp median septum. In old shells the cavities between the brachioophore supports and the floor of the valve are filled up with adventitious shell, causing the development of a structure simulating a sessile cruralium. In reality, however, in young shells the brachioophore supports in their line of attachment with the septum curve ventrally so that their anterior ends rise to a point on the summit of the septum. The cardinal process has a simple shaft that thickens toward the front and merges with the median ridge to form a continuous septum, the thickening at the front of the cruralium being the only mark of union of the two septa. The myophore in old shells is a triangular thickening of the shaft at the posterior, the compressed sides of the triangle bearing the crenulations or marks of muscle attachment. The median ridge usually extends to about the middle of the valve as is usually the case in the orthids. The muscle field is rather narrow, elongate oval, with the posterior adductor scars the larger. Each anterior mark is bipartite as in many other orthid genera. Elevated,

¹²⁶ Pal. N. Y., vol. 8, pt. 1, p. 217.

thickened margins similar to those occasionally seen in Devonian *Schizophoria* are not infrequent in *Linoporella*.

Linoporella is represented by a single species in the Gotland of Sweden and by a closely related form in the Niagaran of the United States. Reed¹²⁷ states that *Orthis polygramma pentlandica* Davidson has pits between the costellæ as in *Linoporella*, but all of the figures indicated by him display neither the external outline and profile nor the internal characters of the genus under discussion. Hence we feel that this species can not be placed in association with *Linoporella*. *Orthis turgida* McCoy, on the other hand, has the external outline and profile and most of the internal features of the genus we are here proposing. Davidson's figures¹²⁸ show the cruralium exactly as it is in *Linoporella*, and in the ventral valve (fig. 20a) the muscle area is somewhat more expanded than is typical in our genus. In the descriptions and figures, however, there is no mention of the external pits so characteristic of *L. punctata*. However, we refer *O. turgida* to *Linoporella* with a query because of the close similarity of internal structure, which we consider of more generic importance than the external ornamentation.

Genus ORTHOTROPIA Hall and Clarke 1894

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1894, pl. 84, figs. 3-7.

GENOHOLOTYPE.—*O. dolomitica* Hall and Clarke 1894.

DESCRIPTION. *Exterior*.—Shell rather small, hinge-line straight, narrow; cardinal extremities obtuse. Lateral profile unequally biconvex, the ventral valve having the greater convexity. Anterior commissure faintly uniplicate. Ventral interarea long, apsacline; beak curved. Delthyrium probably open. Dorsal interarea short, anacline; notothyrium open. Nature of shell substance and external surface unknown.

Ventral interior.—Dental plates prominent, discrete. Muscle field elevated at the front end by a callosity which forms a prominent pseudospondylium. Diductor tracks narrow; adductor field narrow, elevated on a low ridge in old shells.

Dorsal interior.—Notothyrial cavity deep. Brachiphore plates convergent, forming a cruralium with the median septum, which is thin. Adductor field suboval. Cardinal process a simple ridge, possibly with expanded myophore.

GEOLOGIC RANGE.—Silurian (Racine dolomite). The genotype is the only known species.

DISCUSSION.—*Orthotropia* has been well figured but never has been adequately described. Since the genus was made known it has been erroneously classified among the Pentameracea, with which it has no relationships. *Orthotropia* appears to be most closely related to *Linoporella*, having in common with it a pseudospondylium, a cruralium, and a simple orthoid cardinal process (so far as could be determined from the specimens studied).

The only known specimens of *Orthotropia* are in the form of internal molds preserved in a hard dolomite. This is the type of specimen that was available to Hall and Clarke and also the kind preserved in the Teller Collection at the National Museum. The external sculpture and the shell substance are therefore unknown. This being the case, it has been impossible to determine the exact relationships of *Orthotropia* to *Linoporella*. Should the shell substance prove to be punctate and the surface to have the characteristic linoporellid pores, our genus must become a synonym of *Orthotropia*. However, in the absence of this important information it has seemed best to designate the group of *Orthis punctata* as a new genus.

Family TROPIDOLEPTIDÆ, n. fam.

(Tropidoleptinæ Schuchert 1896)

Genus TROPIDOLEPTUS Hall 1857

Hall, N. Y. State Cab., 10th Rept., 1857, p. 151, figs. 1, 2; Ibid., 20th Rept., 1867, p. 280.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, p. 302.

GENOHOLOTYPE.—*Strophomena carinata* Conrad 1839, 3d Ann. Rept., N. Y. Geol. Surv., p. 64.

In this family there is a single genus, *Tropidoleptus*, which, because of its anomalous structure, has been buffeted about between the Strophomenacea and the Terebratellidæ of the Terebratulacea. It is not the purpose here to redescribe the anatomy of *Tropidoleptus*; this has been done very adequately by Hall and by Hall and Clarke. It is our purpose, however, to make some suggestions regarding the taxonomic position of the genus. The anomaly in *Tropidoleptus* is the early appearance of what looks like a terebratelliform loop, and this character has been taken by some workers as proof of relationship with the Terebratellidæ. It was early held that the Devonian genus *Tropidoleptus* was the forerunner of the Terebratellidæ, neglecting the fact that the latter division did not appear till Mesozoic time, an enormous time interval that in itself is strong evidence against any relationship between the genus under discussion and the Terebratellidæ.

In the 1913 edition of Zittel-Eastman, *Tropidoleptus* was placed in association with the Strophomenacea,

¹²⁷ Trans. Roy. Soc. Edinburgh, vol. 51, pt. 4, 1917, p. 857.

¹²⁸ Brit. Foss. Brach., vol. 3, pt. 7, pl. 32, figs. 19a, 20a.

where its position is equally anomalous with the one described above. The presence of endopunctæ at once rules the genus out of the Strophomenacea (Kozłowski having shown that the shell substance of the strophomenoids is impunctate), and there are therefore only two possible places to put it, either in the Dalmanellacea or in the Terebratulacea. It appears to us now, after a long study of the orthoid genera, that the best—at any rate, the least anomalous—position is in the Dalmanellacea. We would place it here because of the punctate shell, the open delthyrium, and the general orthoid nature of the brachial processes, which was suggested by Hall long ago. The endopunctæ of *Tropidoleptus* are very similar to those of *Dalmanella* and allies, but are not so close to those of the Terebratulacea in pattern, the latter being much more dense.

The structure of *Tropidoleptus* accords well with that of the dalmanelloids in having an open delthyrium, a wide hinge-line, and an interarea on both valves. In the dorsal valve there is a small chilidium such as one finds in *Heterorthis* and other punctate genera.

The ventral musculature is suggestive of the orthids, as Hall pointed out. In the dorsal valve the cardinal process is bilobed but is not of the type common in *Strophomena* and allies, in which the lobes are usually isolated. The teeth and sockets are grooved much as in *Parmorthis* among the dalmanelloids. The so called loop is of course the most difficult structure to account for. This in itself, however, does not have the appearance of the true terebrateloid loop that grows out from the septum and unites with the descending lamellæ of the crura; rather these processes are nothing other than very long crura as in some *Rhynchonellas*, but instead of remaining free they appear to unite with the median septum. We hold that this type of arm support could have developed many times, instead of but once. In conclusion, then, we believe that *Tropidoleptus* is a highly specialized and terminal dalmanelloid of short geological life.

At present it is difficult to say definitely out of what dalmanelloids *Tropidoleptus* may have come, but we suggest that it may have been out of the *Parmorthis* stock.

PART V. THE GENERA OF THE SUBORDER PENTAMEROIDEA

Derived out of the Orthacea, the Pentameroidea retain their impunctate tests, but most of them tend with time to lose more and more of their transverse shells with wide interareas and to become elongate and subrostrate, smooth or costate, with well developed spondylia and characteristic cardinalia. The delthy-

rium is usually open but may be modified by deltidia or marginal thickenings.

The Pentameroida begin in the Middle Cambrian and die out with the Devonian. They include the superfamilies Syntrophiacea Schuchert and Cooper and Pentameracea Schuchert.

Superfamily SYNTROPHIACEA Schuchert and Cooper 1931

Specializing Protremata derived out of the Orthacea (probably the ancestral stock of the Billingsellidae), developing a more or less lobate exterior, interiors with either pseudospondylia or spondylia of the simplex type, and occasionally cruralia. Cardinal process absent or rudimentary. Delthyrium and notothyrium open. Test fibrous, impunctate.

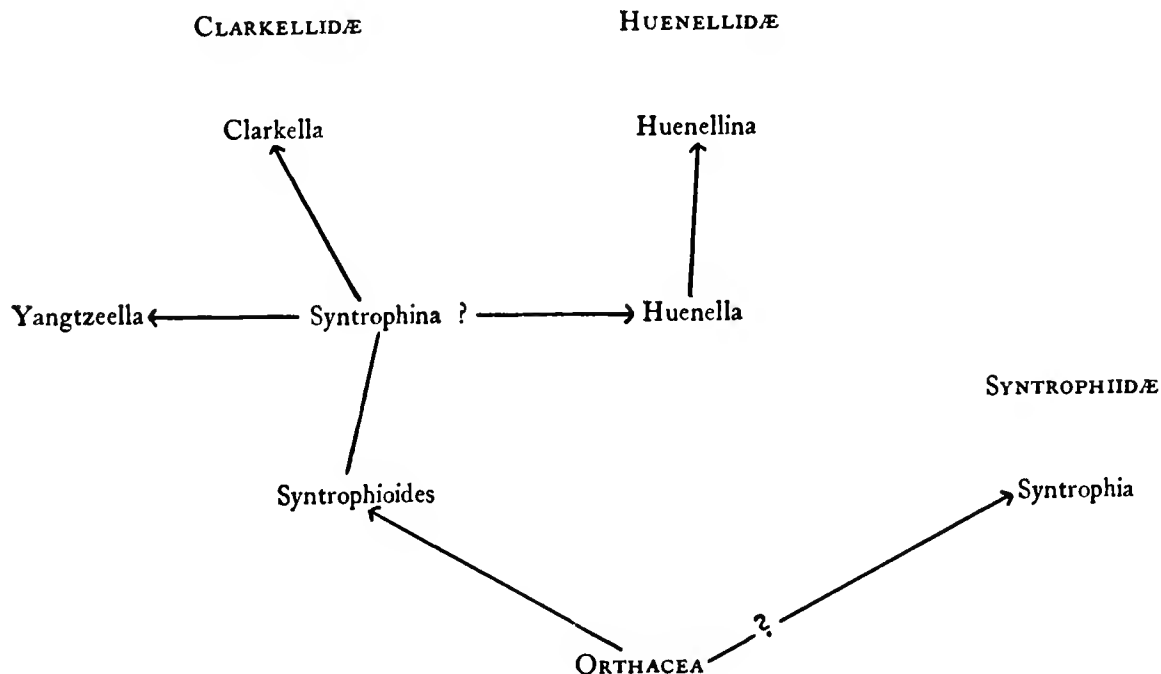
GEOLOGIC RANGE.—Middle and Upper Cambrian, Ozarkian, and Lower Ordovician.

Embraces the Clarkellidæ, Syntrophidæ, and Huenellidæ.

The Syntrophiaea may have given rise to the Pentameracea. It is probable that the other stocks with simple spondylia—the Clitambonacea—arose in the Billingsellidæ, retaining and developing more fully the shell form, chilidium, and perforate deltidium; in other words, remaining more like Orthacea than Pentameracea.

The genetic relations of the Syntrophiaceae are thought to be as shown in Table 16.

Table 16



(probably out of an early Middle Cambrian ancestor of the Billingsellidæ)

Family CLARKELLIDÆ Schuchert and
Cooper 1931

Syntrophiacea, externally like *Syntrophina* and with a spondylium simplex or a pseudospondylium. In the dorsal valve the brachioophore supports are divergent, discrete plates. Ventral pallial markings as in *Billingsella*.

GEOLOGIC RANGE.—Middle Cambrian to Lower Ordovician.

Embraces the following genera:

Syntrophioides Schuchert and Cooper
Syntrophina Ulrich
Clarkella Walcott
Yangtzeella Kolarova

Genus SYNTROPHIOIDES Schuchert and
Cooper 1931

Pl. 15, figs. 20, 23

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 247.

GENOHOLOTYPE.—*Billingsella harlanensis* Walcott 1905, Proc. U. S. Nat. Mus., vol. 28, p. 236; Camb. Brach., 1912, p. 746, pl. 87, figs. 5-5d (as *Wimanella harlanensis*).

DESCRIPTION. *Exterior*.—Subelliptical to subsemi-elliptical, hinge-line straight; cardinal extremities usually obtusely angular; lateral profile biconvex; anterior commissure uniplicate; dorsal fold not greatly pronounced. Ventral interarea long, apsacline, delthyrium open; surface marked only by fine, concentric lines of growth. Test probably fibrous, impunctate.

Ventral interior.—Delthyrial cavity rather shallow, dental plates in the type specimens not sharply marked; musculature clearly billingselloid, having a prominent central adductor track which widens toward the front and is cleft into halves by a low ridge; the front of the adductor track elevated slightly. Diductor tracks smaller than the adductor ones, rounded in front, separated from the latter by low ridges. From the anterior ends of the diductors two pairs of pallial sinuses extend in an antero-lateral direction nearly to the front border as in *Billingsella*.

Dorsal interior.—Notothyrial cavity shallow, brachioophore plates convergent and resting on the floor of the valve (?); musculature prominent, posterior adductors larger than the anterior pair, suboval in outline; anterior pair about half the size of the posterior one. Two pallial sinuses have their origin at the point of contact with the posterior adductors in the mid-line of the shell and are separated by a slight median elevation. They extend in this closely appressed condition as far as the front margins of the anterior adductors,

where they branch abruptly toward the antero-lateral margins.

GEOLOGIC RANGE.—Middle Cambrian of Tennessee with *Billingsella* (or *Wimanella*) *harlanensis* Walcott and ? *B.* (or *W.*) *saffordi* Walcott.

DISCUSSION.—This genus is readily separated from *Billingsella* by its concentrically marked surface, syntrophiid form, and dorsal musculature. *B. harlanensis* was placed in *Wimanella* by Walcott because of its smooth shell, but since that genus appears to have a costellate surface, the species under consideration can not be left there.

The dorsal musculature of *Syntrophioides* is well defined and strongly suggests that seen in *Syntrophina* and *Clarkella*, representing a divergence probably out of some ancestor of the Billingsellidæ of the early Middle Cambrian. In these circumstances we see how the slight generic differences in these early Cambrian forms may have given rise to later independent families and even superfamilies.

Genus SYNTROPHINA Ulrich 1928

Pl. 15, figs. 1, 2, 15-19, 30, 31

Ulrich in Weller and St. Clair, Missouri Bur. Geol. Mines, 2d ser., vol. 22, 1928, p. 74 (without description).

GENOHOLOTYPE. — *Syntrophina campbelli* Walcott 1912, Camb. Brach., pp. 801-802, t. figs. 73A-F.

DESCRIPTION. *Exterior*.—Subelliptical, hinge-line narrower than the greatest width of the shell; cardinal extremities rounded. Lateral profile strongly biconvex; ventral valve deeply sulcate, dorsal valve with a prominent fold; anterior commissure uniplicate. Ventral palintrope short, apsacline; delthyrium open. Dorsal interarea shorter than the ventral, apsacline to anacline; notothyrium open. Surface marked only by fine concentric lines of growth. Test fibrous, impunctate.

Ventral interior. — Delthyrial cavity deep, teeth strong, dental plates convergent, forming a true spondylium simplex. Muscle impressions borne on the upper surface of the spondylium; diductor marks on the sides and floor of the spondylium at the back; adductor impressions (?) in front of the diductor scars at the narrow end of the spondylium. Pedicle callist at the posterior. Pallial marks two broad trunks extending antero-laterally from beneath the spondylium. Umbonal cavities and umbo-lateral spaces marked by low radial ridges. Complete or incomplete accessory septa occur in the vicinity of the spondylium in some specimens and show a convergence toward *Clarkella*.

Dorsal interior.—Notothyrial cavity deep, brachioophores long, brachioophore supports divergent, extending to the floor of the valve. Cardinal process rudimentary, elevated on a narrow shelf at the posterior of the notothyrial cavity. Posterior adductor scars the

larger, situated a little outside the anterior pair. A prominent pallial sinus extends antero-laterally from the anterior end of each adductor muscle impression.

GEOLOGIC RANGE.—Upper Cambrian to Lower Ordovician of North America.

AMERICAN SPECIES

Syntrophina 3 n. spp. (Ulrich Coll.)

Syntrophia campbelli Walcott 1908

S. isis Walcott 1924

S. nundina Walcott 1905

S. palmata Cleland 1900

S. perilla Walcott 1924

S. rotundata Walcott 1905

? *Triplexia primordialis* Whitfield 1877

DISTINGUISHING CHARACTERS.—*Syntrophina* may be recognized by its external resemblance to *Syntrophia* and by the presence of a ventral spondylium, but differs in having two dorsal divergent brachiophore supports and consequently no cruralium simplex.

DISCUSSION.—Interesting features of this genus are the well defined muscle marks on the dorsal side of the spondylium, the peculiar shelf at the posterior of the notothyrial cavity, and the dorsal muscle and pallial marks. Internal molds from Phillipsburg, Quebec, preserving the spondylia, show on them a median ridge toward the anterior, which widens and becomes somewhat more elevated, terminating at the back end of the median septum. This anterior ridge or elevation may represent the impression of a deeply sunk adductor track. Behind the "adductor track," and surrounding it partially, are the probable impressions of the diductor muscles on the floor and sides of the spondylium (see pl. 15, fig. 15). The correct identification of these muscle marks is attended with some difficulty, but the suggested arrangement would be in accord with the mechanics of opening or closing a brachiopod shell and would homologize with the same marks seen in valves not provided with a spondylium.

In the dorsal valve the brachiophores project for some distance into the valve and are supported by stout plates which show as subparallel or slightly divergent slots on internal molds (see pl. 15, figs. 2, 17, 19, 30). These plates form the lateral walls of a deep notothyrial cavity, which has at the back end a low shelf built on the sides of the brachiophore supports and the posterior slope of the notothyrial depression. In the mid-line of the valve and the shelf at its back end there is in some specimens a low median elevation, interpreted as the cardinal process (pl. 15, figs. 30, 31). This shelf and the cardinal process probably mark the seat of attachment of the diductor muscles.

The adductor muscle scars are thickened at their front ends and give off broad pallial sinuses that extend toward the antero-lateral extremities of the valve. The musculature of *Syntrophina* strongly resembles that of *Syntrophoides* and *Finkelburgia*.

The genus *Syntrophina* has a long series of species (mostly undescribed) continuous from the Upper Cambrian into the Lower Ordovician. So far as known there are no *Syntrophia* s. s. in the Cambrian or Ozarkian. It is true that Walcott considered *S. rotundata* as the Cambrian representative of *Syntrophia*, but this appears not to be correct, since the type specimens in the United States National Museum have the characters of *Syntrophina*. The reference of the species to *Syntrophia* is due to Walcott's mistaking a ventral valve for a dorsal, thereby giving the essential structure of *Syntrophia*. Other specimens in the same lot (Cat. No. 52493), however, have the features of *Syntrophina*.

Ulrich's new genus *Syntrophinella*, as yet undescribed, is internally like *Syntrophina* but is multicostellate externally. Its genotype is *S. typica*, n. sp., illustrated on our plate 15, figures 4, 5, 13.

Genus CLARKELLA Walcott 1908

Pl. 15, figs. 6-11

Walcott, Smiths. Misc. Coll., vol. 53, 1908, p. 110;
Camb. Brach., 1912, p. 809, pl. 104, figs. 2-2d.

GENOHOLOTYPE.—*Polytaechia* ? *montanensis* Walcott 1905, Proc. U. S. Nat. Mus., vol. 28, p. 295.

DESCRIPTION. *Exterior.*—Like *Syntrophia*, with a prominent fold and sulcus. Test fibrous, impunctate.

Ventral interior.—There is a spondylium simplex but in some species it is supported by two or more lateral accessory septa. Two strong divergent pallial sinuses extend antero-laterally from the umbonal cavities.

Dorsal interior.—Essentially like that of *Syntrophina*, but there are accessory lateral septa, at most two in number, which are united with the descending brachiophore supports. There are six pallial sinuses radiating from the umbonal cavities and in front of the muscle area.

GEOLOGIC RANGE.—Upper Cambrian (Ozarkian).

AMERICAN SPECIES

Polytaechia montanensis Walcott 1905

Syntrophia nonus Walcott 1924

DISTINGUISHING CHARACTERS.—The character which gives *Clarkella* generic standing is the structure of the cardinalia with its prominent accessory plates.

DISCUSSION.—In the original definition of the genus, Walcott described spondylia in both valves, supported by accessory septa. This structure can not be questioned in the ventral valve, since there is here a spondylium simplex supported by a stout median septum and two or more accessory septa. The latter are, however, not universally present, being lacking in *S. nonus*.

(Walcott). In the dorsal valve there is no cruralium as Walcott has described and illustrated. Instead of there being a continuous spoon-shaped plate supported by lateral septa, there are two plates beneath the brachiphores which converge medially but never unite. Each plate is supported by two or more septa, the usual number being two, one inner and one outer (see pl. 15, figs. 7, 10).

Clarkella is evidently very closely related to *Syntrophina* and is characteristic of the Ozarkian. It is widely distributed geographically, being known from Montana, British Columbia, and Phillipsburg, Quebec.

plex which is supported for nearly its entire length by a septum which is short and thick; septum extending for half the length of the valve. There are accessory lateral septa up to four in number aiding in the support of the spondylium. Between these are other low radial ridges.

Dorsal interior.—Notothyrial cavity deep; sockets deep, at the posterior the brachiphore plates form a small, deep, spoon-shaped muscle platform supported at the back by one or two pairs of lateral septa. After a short distance the platform, which is evidently for the attachment of the diductors, ends, but the two lateral

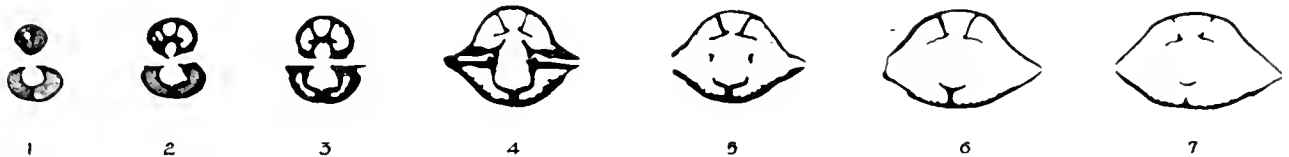


FIG. 22.—*Yangtzeella poloi* (Martelli). Serial sections through the beak of a mature shell. The internal structure allies this genus with *Clarkella* Walcott and proves conclusively that it has no relationships with *Triplexia*. The stippled areas indicate adventitious shell substance which fills the umbonal chambers of both beaks. Such a filling is common in many genera of spondylium-bearing shells. The shell sectioned was 19.3 mm. in length. All structures disappeared 8.5 mm. from the beak. Distances from beak:

| | |
|-----------|-----------|
| 1—1.4 mm. | 5—5.8 mm. |
| 2—2.5 | 6—6.8 |
| 3—3.2 | 7—7.3 |
| 4—4.5 | |

Genus YANGTZEELLA Kolarova 1925

Pl. 15, figs. 24-26; t. figs. 22, 23

Kolarova, Bull. Geol. Soc. China, vol. 4, 1925, p. 219, pl. 1, t. fig. 1.

GENOHOLOTYPE.—*Triplexia poloi* Martelli 1901, Bull. Soc. Geol. Ital., vol. 20, fasc. 1, pp. 302-304, pl. 4, figs. 13-22.

DESCRIPTION. *Exterior*.—Outline subquadrate, hinge-line straight, narrower than the total width of the shell; cardinal extremities rounded; lateral profile biconvex, the dorsal valve having the greater convexity. Anterior commissure uniplicate; ventral sulcus very deep, defined only on the front half of the shell; dorsal fold pronounced only in the anterior area. Ventral interarea longer than the dorsal, apsacline; beak curved slightly and may or may not be resorbed by pedicle pressure; delthyrium open. Dorsal interarea curved, apsacline, beak strongly curved, umbo inflated, notothyrium open. Surface nearly smooth, marked by concentric growth-lines and distant lamellæ, and by faint radiating ridges. Test fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth strong; dental plates thick, forming a spondylium sim-

septa persist, each bearing a laterally directed shelf and a rather long brachial process.

GEOLOGIC RANGE.—The only known species is *Y. poloi* (Martelli) of the ? Lower Ordovician of China.

DISTINGUISHING CHARACTERS.—The chief diagnostic characters of *Yangtzeella* are its nearly smooth exterior, *Triplexia*-like or syntrophoid outline and profile, ventral spondylium simplex which may be supported by two or four accessory lateral septa, and in the dorsal valve a spoon-shaped plate supported by two primary lateral and two accessory lateral septa. It is impossible to say whether or not this plate bore muscles.

DISCUSSION.—*Yangtzeella* shows several interesting features. One of these is the great amount of adventitious shell substance deposited in the umbonal cavities of the valves, chiefly in the ventral one. In Kolarova's sections (his pl. 1, figs. 2-6) the ventral shell for about 3 mm. from the beak is wholly test, and the same is true of the Yale specimens for 2.8 mm. from the beak. However, the septa show clearly in the adventitious substance so that none of the shell anatomy is obscured in the sections.

The supporting plate beneath the ventral spondylium is commonly split or fractured so that it appears to be a duplex septum, and yet it is not precisely like the

duplex septum of *Pentamerus*, but is single as in *Climacambonites* or *Vellamo*, which occasionally also have the septum fractured medially. The spondylium is supported for practically its whole length and there are generally two lateral septa as in some species of *Clarkella*. At its front end the spondylium hangs free of the septum, which is prolonged forward as a ridge on the floor of the valve. Between the main septa on the floor of the valve are numerous accessory radiating ridges, such as are common in *Syntrophina* and *Clarkella*. These radiate from each of the umbonal cavities, the larger ones forming the septa. They are interpreted by Kolarova as ridges or septa between the diductor muscles. According to our view, they are



FIG. 23.—*Yangtzeella poloi* (Martelli). Section cut through an adult specimen, showing septa of both valves and notothyrial chamber of the dorsal valve. \times about 4.

for attachment of the ovarian bodies, and so far as our knowledge goes, the ventral muscle marks in spondylium-bearing shells are always located on the upper or dorsal surface of the spondylium, and such shells never have additional muscle-scars on the valve floor. Low ridges upon the spondylium of *Yangtzeella* suggest that the muscles here were also attached to the upper surface of the spondylium.

The dorsal valve is especially interesting and quite unlike any other brachiopod except *Clarkella*. There is a narrow, spoonlike platform supported by two lateral septa, and two or more accessory ones. After about 3.5 mm. in a specimen 20 mm. long, the spoon terminates, but the lateral septa persist and are overlain by horizontal plates or shelves that may or may not be supported by septa. The brachiophores consist of rather long processes extending into the valve from the extremity of the brachiophore plates, as in *Syntrophina*.

This shell was originally referred to *Triplesia* and in the 1929 classification of Schuchert was placed in association with this and allied genera. *Yangtzeella*, however, has no forked cardinal process, and besides, the presence of a spondylium and cardinalia like those of *Clarkella* shows that it belongs with the Syntrophidae,

where Miss Muir-Wood placed it.¹ It is closest to *Clarkella* in a broad sense, having many septa in each valve. However, *Clarkella* does not have a spoon-shaped dorsal plate or lateral processes such as occur in *Yangtzeella*.

Family SYNTROPHIIDÆ Schuchert 1896

Smooth biconvex Syntrophicea having well developed interareas, a spondylium simplex, and a cruralium simplex.

GEOLOGIC RANGE.—Lower Ordovician.

Embraces but one genus, *Syntrophia* Hall and Clarke. Walcott has referred to this family his *Swantonina*, a genus whose taxonomic position is wholly unknown, but we leave it here as we are not able to place it.

Genus SYNTROPHIA Hall and Clarke 1891

Pl. 15, figs. 3, 27-29, 32

Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1891, p. 270; pt. 2, 1893, p. 216, pl. 62, figs. 1-10.

GENOHOLOTYPE.—*Triplesia lateralis* Whitfield 1886, Bull. Amer. Mus. Nat. Hist., vol. 1, no. 8, p. 303, pl. 24, figs. 9-11.

DESCRIPTION. *Exterior*.—Transversely oval, hinge-line narrower than the greatest width, cardinal extremities obtuse; lateral profile biconvex; anterior commissure uniplicate; fold and sulcus usually shallow; areas on both valves; ventral interarea apsacline, delthyrium open; dorsal interarea anacline, notothyrium open. Surface marked only by fine concentric lines of growth. Test fibrous, impunctate.

Ventral interior.—"Teeth small"; dental plates uniting with a median septum to form a spondylium simplex that is free at its anterior end. Muscle confined to the spondylium.

Dorsal interior.—Much like the ventral, the brachiophore supports converging and uniting with a median septum to form a cruralium. Pallial trunks radiating from the muscle area as in *Syntrophina*.

GEOLOGIC RANGE.—The only known species is the genotype, which comes from the Lower Ordovician (upper Beekmantown) of Vermont.

DISTINGUISHING CHARACTERS.—The presence of a spondylium and a cruralium is the chief distinguishing feature.

DISCUSSION.—When Hall and Clarke based *Syntrophia* on *Triplesia lateralis*, they were struck most by the external form and the presence of a spondylium.

¹ Zool. Record, 1926.

For these reasons they included in the genus many similar species, making, as we now see, a rather heterogeneous lot of shells. Since *Triplexia lateralis* is the genotype, the name must be based upon it, and as so restricted, all of the other species formerly placed here must be taken out of the genus.

Specimens of *Syntrophia* are exceedingly rare and none were available to us for sectioning. It is therefore not known with certainty whether the genus possessed a spondylium simplex or one of the duplex type. Polished specimens in the National Museum at Washington do not show a suture line in the septum of the spondylium, hence the presumption is that the latter was of the simplex type.

? Genus SWANTONIA Walcott 1905

Walcott, Proc. U. S. Nat. Mus., vol. 28, 1905, p. 296; Camb. Brach., 1912, p. 796, pl. 104, figs. 5-5b.

GENOHOLOTYPE. — *Camerella antiquata* Billings 1861, Pal. Foss., vol. 1, pp. 10-11, fig. 13.

DESCRIPTION. *Exterior*.—The species and genus are based on a single ventral valve. Shell ovate, moderately convex, substrate, with a shallow sulcus toward the front; multicostate (8-12 costæ). Interarea narrow and long; delthyrium open; teeth rudimentary, muscle-scars not preserved.

GEOLOGIC RANGE.—Lower Cambrian of Swanton, Vermont (*S. antiquata* (Billings) 1861) and Nevada (*S. weeksi* Walcott 1905).

DISCUSSION.—There is some superficial resemblance here to *Camerella*, but the internal structure is very different. According to Walcott, *S. antiquata* has a "narrow, strong, concave shelf or area; the area or shelf is free from contact with the bottom of the valve, a recess or chamber existing beneath it." This feature he has taken to indicate a free spondylium, but the presence of such a structure may be questioned. The specimen is preserved as a mold of the interior. In the vicinity of the beak the specimen is indented on each side, the indentation representing the position of the lateral interareas. Immediately under the beak, however, there is no excavation such as would be expected if there were a free spondylium, and the internal mold is united to the matrix rock just as if there were an open delthyrium now filled up. Were it not for the strong costæ on the outside of the shell, the position of *Swantonina* among articulate brachiopods might be questioned.

Swantonina therefore appears to be a narrow-hinged form without a spondylium, but its family position can not at present be determined, especially in the absence of any knowledge of the dorsal valve. *S. weeksi* is also based on a single ventral valve, and shows external characters only. However, as Walcott referred the genus to the Syntrophiidæ, we will leave it here provisionally.

Family HUENELLIDÆ Schuchert and Cooper 1931

Syntrophacea externally like *Syntrophia* but costate or costellate. Ventral valve with a pseudospondylium; dorsal brachiophore plates discrete, subparallel.

GEOLOGIC RANGE.—Upper Cambrian and Ozarkian.

Embraces but two genera, *Huenella* Walcott and *Huenellina* Schuchert and Cooper.

Genus HUENELLA Walcott 1908

T. fig. 24

Walcott, Smiths. Misc. Coll., vol. 53, 1908, p. 109; Camb. Brach., 1912, p. 804, pl. 103, figs. 1-1i.

GENOHOLOTYPE. — *Syntrophia texana* Walcott 1905, Proc. U. S. Nat. Mus., vol. 28, p. 294.

DESCRIPTION. *Exterior*.—Subelliptical in outline; hinge-line straight, always narrower than the total width of the valves; cardinal extremities rounded. Lateral profile biconvex. Anterior commissure unipligate; dorsal fold broad in front, prominent; sulcus deep. Ventral interarea longer than the dorsal, apsacline, delthyrium open; dorsal interarea anacline, notothyrium open. Surface costate or costellate, especially toward the front. Test fibrous (?), impunctate.

Ventral interior.—Delthyrial cavity deep; teeth strong and somewhat elongate; dental plates well developed, converging to the floor of the valve to form a pseudospondylium which bears the muscle-scars. Two broad pallial trunks diverge antero-laterally from either side of the pseudospondylium and follow the shell sulci nearly to the front margin.

Dorsal interior.—Notothyrial cavity deep; brachiophore supports short, convergent, but cemented directly to the floor of the valve. At the anterior they are extended forward and laterally as low ridges which separate the anterior from the posterior adductor scars. Cardinal process simple, very faintly visible or absent. Adductor impressions elongate, tear-shaped or oval, directed antero-laterally. A pallial sinus is given off from the anterior extremity of each adductor impression. The inner trunks extend along the margins of the sulcus, while the outside trunks pass along the anterior portion of the lateral lobes.

GEOLOGIC RANGE.—Upper Cambrian and Ozarkian of North America.

SPECIES

Costate section

Huenella abnormis (Walcott) 1905

H. billingsi (Walcott) 1905

H. hera Walcott 1924

H. texana (Walcott) 1905

H. texana laeviusculus (Walcott) 1905

Costellate section

H. icetas Walcott 1924*H. juba* Walcott 1924*H. lesleyi* Walcott 1908? *H. simon* Walcott 1924? *H. vermontana* Walcott 1912? *H. weedi* Walcott 1924? *Hebertella battis* (Billings) 1865

DISTINGUISHING CHARACTERS.—*Huenella* is recognized most readily by its syntrophinoid outline and profile, costate or costellate exterior, pseudospondylium, convergent brachiophore supports, and dorsal musculature.

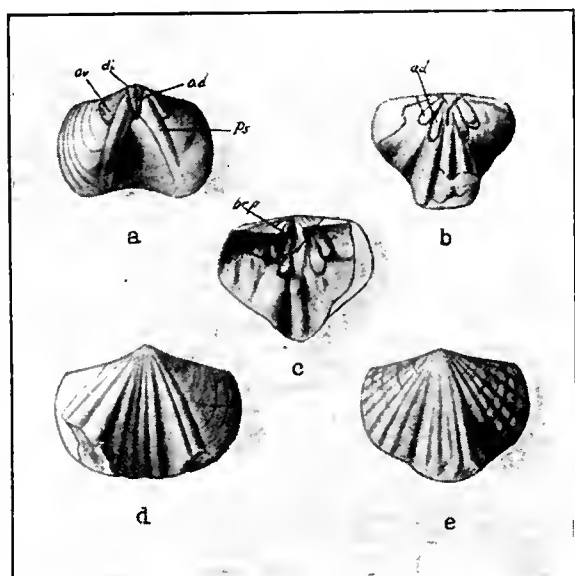


FIG. 24.—a-c, *Huenella abnormis* (Walcott). a, ventral internal mold, showing muscular impressions on the imprint of the spondylium. b, c, dorsal internal mold and interior, showing musculature and brachiophore plates (*brp*). *ov*, ovarian impressions (mistaken by Walcott for muscle marks); *di*, diductor impressions; *ad*, adductor impressions; *Ps*, pallial sinus.

d, e, *H. texana* (Walcott), ventral and dorsal exteriors, showing coarse ribbing and strong fold and sulcus.

After Walcott 1912, pl. 103.

DISCUSSION.—*Huenella* differs from *Syntrophina* and *Syntrophina* not only in the external costation but also in internal characters. Internally there is a pseudospondylium bearing the muscle impressions; at the front it is elevated slightly on a prominent thickening of secondary shell. From the musculature of *H. abnormis* the myology of this genus would appear to be essentially the same as that of *Syntrophina*. However, the diductor and adductor scars are not flabellate impressions outside the pallial trunks as Walcott describes

and figures in that species (1912, p. 806, pl. 103, fig. 2b). As he figures these impressions, the adductor scars are posterior to the diductors; their position and arrangement are accordingly unlike the ventral musculature of any other known brachiopod. Walcott has evidently mistaken impressions that are in the position of, and are usually considered to be, ovarian impressions. Furthermore, in the same figure the musculature is shown clearly on the floor of the pseudospondylium and is essentially the same as that which is seen commonly in *Syntrophina*.

This genus as now constituted may be divided into two groups on the basis of the external ornamentation, as shown above.

H. simon and *H. weedi*, according to their external form and sculpture, suggest affinities with *Billingsella* rather than with *Huenella*.

Genus HUENELLINA Schuchert and Cooper 1931

Pl. 15, figs. 14, 21, 22

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 247.

GENOHOLOTYPE.—*Huenella triplicata* Walcott 1924, Smiths. Misc. Coll., vol. 67, no. 9, p. 526, pl. 125, figs. 1-15.

DESCRIPTION. *Exterior.*—Externally much like *Platystrophia*, being strongly sulcate and costate. Hinge-line shorter than the greatest width of the shell, and interareas well developed on both valves. Delthyrium and notothyrium open.

Ventral interior.—Delthyrial cavity deep, teeth strong and long, with well defined crural fossettes; dental plates strong; pseudospondylium scarcely elevated in front. Adductor impression subcircular, diductor scars indefinite. Umbo-lateral spaces marked by elevated subradial ridges.

Dorsal interior.—Notothyrial cavity deep, brachiophores long, curved slightly; brachiophore supports prominent, curved, and extending directly to the floor of the valve; cardinal process rudimentary or absent. Attached to the outside of the brachiophores and the lower (anterior) side of the palintrope is a lateral septum which extends obliquely toward the lateral margins.

GEOLOGIC RANGE.—Upper Cambrian (Ozarkian) of Novaya Zemlya, Arctic Russia. The only known form is *H. triplicata* (Walcott).

DISCUSSION.—The main distinction between this genus and *Huenella* is to be found in the lateral septa developed under the anterior part of the dorsal palintrope. There is nothing among the Cambrian brachiopods exactly like this feature and it is difficult to understand what purpose it could have served other

than additional strengthening of the palintrope. The brachiophore supporting plates are well developed, discrete, and convergent toward the floor of the valve, defining a rather deep notothyrial cavity. The brachiophores, judging by internal molds, were long, slender processes extending from the point of union of the accessory septal plate and the palintrope.

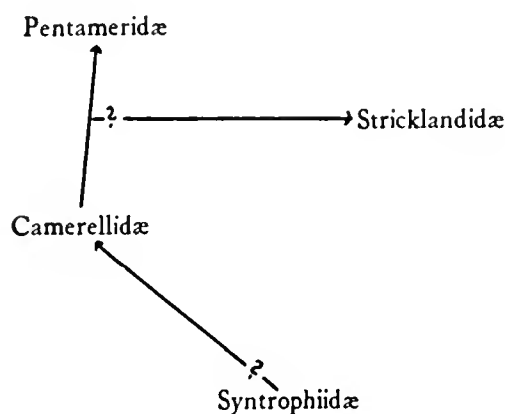
In the ventral valve a feature of particular interest

is the shallow pit at the front end of the pseudospondylium. Such a pit also occurs in *Syntrophina*, and is in exactly the same position as the anterior adductor scar in *Billingsella*. Behind this pit can be seen the central adductor track and on each side of this, impressions which are regarded as diductor scars. This antero-central pit may represent the final place of the adductor scar in its forward migration during growth.

Superfamily PENTAMERACEA Schuchert 1896

Specializing Protremata probably originating in the Syntrophicea (family Syntrophiidæ), characterized by spondylia that in the primitive families are nearly always supported by single septa (= spondylium simplex) and in the derived families by double septa (coalesced septal plates = spondylium duplex), but in rare instances in any of the families may hang free

Table 17



or posteriorly supported by a remnant of the septum. The more important family characters occur in the dorsal cardinalia, which may be discrete or medially coalesced into a cruralium that bears the adductor muscles. Cardinal process usually absent, or rudimentary as a linear ridge or slight boss. Rudimentary or modified remnants of the deltidium occur rarely, and chilidia never. Shells narrow-hinged, with small interareas, or decidedly rostrate with plane areas; exterior smooth, costate or multicostate. Test fibrous, and, so far as known, without endopunctæ.

GEOLOGIC RANGE.—Middle Ordovician to close of Devonian.

Embraces the following families:

- Camerellidæ Hall and Clarke
- Pentameridæ McCoy
- ? Stricklandidæ Hall and Clarke

The genetic relationships appear to be as shown in Table 17.

After completing their survey of the great group of orthids, the writers turned naturally and logically to a study of the Pentameracea. They had embarked on this course and carried on their research for about six weeks when it was interrupted by the removal of the junior author to Washington. This had at once disadvantages and advantages. At Washington it was possible to add observations on the strange genera *Brooksina* and *Harpidium* and on the even more aberrant *Cymbidium*. In the National Museum collections also are some fine specimens of *Orthotrophia* which show the necessity for removal of this genus to the Dalmanellacea near *Linoporella*.

As the presentation of the pentamerids now stands, it represents a survey of two of the finest collections of these shells in this country. However, the work can not be considered as final. In any study such as this, in which the elucidation of internal details depends on the destruction of materials, it would have been desirable to have still more specimens. As an example of this need it might be stated that, in all of the specimens of *Pentamerus* studied, we did not find a single example which retained a deltidium, yet Hall and Clarke reported such a structure. Furthermore, where there was abundance of common species, the rarer forms were represented in each collection by one or two specimens which could not be sacrificed to serial sectioning. Therefore much remains still to be done. We have, however, seen, and in the majority of cases sectioned, specimens representing the genotype of nearly all the pentamerid genera. If nothing else, the study strives to make clear exactly what each genus is, and, as far as possible, to eliminate from each the non-typical species. It has therefore been necessary to create a few new genera. Besides *Orthotrophia*, the probability is that *Stricklandia* will eventually have to be removed from its honored place among the pentamerids. On the other hand, as we have shown on earlier pages, the Porambonitidæ belong with the Orthacea. The old family Pentameridæ is, however, now divided into three, the Camerellidæ, Stricklandidæ, and the very varied Pentameridæ, on the basis of certain internal characteristics. Recent studies by Kozłowski have shown that the Camerophoriidæ are spondylia-bearing Rhynchonellacea.

TECHNIQUE

During the progress of this work, the junior author has improved the old Zugmayer process of serial sectioning so as to leave a remainder of the specimen, and this is highly advantageous. Serial sectioning has heretofore resulted in total destruction of the specimen, or in the destruction of so much of it that the remainder was worthless. In our work we have followed the course described below: Before sectioning, the specimen is measured by micrometer. Sectioning proceeds slowly, the structures being sketched at intervals with the aid of a camera lucida, thus showing the significant changes in spondylia, septa, and cardinalia. This procedure is continued until that plane is reached where the ventral teeth can be seen inserted in the sockets of the dorsal valve. The specimen is then cemented by balsam to a glass slide and the whole measured. Sectioning is now resumed from the anterior end of the shell and continued until the internal lamellæ begin to appear. The specimen is measured, the shell structures sketched, and this procedure followed until the section is too thin to grind further, when it is covered by a glass slip. In this way at least a thin section of the specimen remains to form a record. In sectioning from the anterior end, the distance from the plane where internal structures first appear must be added to the length from the beak to the plane of articulation; addition of the thickness of the thin slice representing the distance from the last plane of the anterior sections to the plane of the articulation must also be made.

In work demanding the sectioning of brachiopod material it is desirable that a replica of the specimen first be made, then the original should be photographed for dorsal, ventral, lateral, anterior, and posterior views, and these photographs should be reproduced along with those of the other type material.

MORPHOLOGY OF THE PENTAMERACEA

The pentamerid is a rather distinctive shell, easily recognized by its usually strongly biconvex valves and its spondylium duplex and elongate median septa in both valves. It was formerly the practice of most writers to place nearly all of the spondylium-bearing shells among the Pentameracea, but recent advances in brachiopod studies, and especially those of Kozłowski, have shown that the spondylium is a rather common structure developed independently and in different ways in many stocks. For example, such an unmistakable orthid as *Enteletes* has been shown by Likharev² to have developed a spondylium in its alteration to *Enteletella*. Among the punctate spiriferids,

Cyrtina has a spondylium, and among the terebratulids *Amphigenia* may be cited. No one would now consent to the union of these genera to the Pentameracea.

Although the spondylium is of itself not a distinctive feature of this group of shells, it is, in combination with certain dorsal structures, a rather important additional character. Considering the Pentameridæ as a whole, there is a distinctive tripartite division of the dorsal septa which is characteristic of the family and appears to be its most important taxonomic feature. The family Camerellidæ does not accord with the characteristic pentameroid dorsal structure and it is for this reason that we have given it family rank. It has singular resemblances to the Syntrophidæ and when material is at hand showing in detail the pallial markings of the Camerellidæ, it may be necessary to make still other family arrangements than those offered in this book. Such material, in the form of internal molds, is singularly lacking in both the collections studied.

We again find among the Pentameracea, as we did among the Orthacea and Dalmanellacea, that dorsal structures are most diagnostic of family and mutual relationships.

The following discussion is designed to summarize the significant points of pentamerid anatomy.

EXTERIOR.—There are several features of the exterior of the pentamerid shell that are of some interest:

1. *Ventricosity.*—Among the Camerellidæ none of the shells are flattish but all are rather globular and the valves strongly gibbous. The Pentameridæ, on the other hand, have a number of stocks that are rather flattish but may have developed gibbous stocks as offshoots. Such, for example, is the development of the subcylindrical *Pentamerus* from the rather flattish *P. oblongus*. *Conchidium* is evidently a strongly gibbous stock from the start and it is difficult to ascertain its ancestry; the best suggestion appears to be that it came out of *Clorinda* or *Barrandella*. In the Gypidulinæ nearly all the genera have at least one valve strongly arched.

2. *Ornamentation.*—It is at present difficult to say whether the first of the pentamerids was smooth, or ribbed as is known to be the case among the orthids. In the Camerellidæ the species of the primitive genus *Camerella* are partially smooth and partially ribbed. It would appear safe to say that this stock started from a smooth one like the syntrophids and subsequently became anteriorly ribbed, since the culminating genus of the family, *Anastrophia*, is the most strongly costate member.

In the Pentamerinæ, on the other hand, the problem is not so easy, since the ribbed and the smooth stocks appear nearly simultaneously, or, as seen from present knowledge, the ribbed stocks have a little the better of it from the point of view of time. Among the Gypidulinæ—*Barrandella*, *Clorinda*, *Gypidula*, and

² Bull. Com. Géol., vol. 45, no. 6, 1924, pp. 720-721.

Sieberella—smooth and costate stocks are essentially contemporaneous, although in America the Barrandellas and Clorindas evidently appear first, in the Brassfield formation. With the Pentamerinæ the first to appear is *Platymerella* (Brassfield-Alexandrian). It may be the forerunner of *Pentamerus*, since the latter nearly always shows broad radial costæ, but whether these represent secondary dying out of stronger costation or incipient development of the same is not known. *Conchidium* was evidently always costate but may have given rise to two secondarily smooth genera.

3. *Interareas*.—It has been the common belief among paleontologists that the pentamerids have lost their interareas. This is certainly in part true. The reduction of the interareas, and their subsequent loss in a few stocks, are consequent upon the narrowing of the hinge-line and the development of rostration. It is very possible that this rostration has gone hand-in-hand



FIG. 25.—*Conchidium biloculare* (Linnæus), from Klintehamn, Gotland. Section showing unusual deltidial cover of ventral valve. See pl. 29, fig. 4. The whole ventral interior, except for the two roughly oval areas on either side of the spondylium, is filled with adventitious shell, represented by the stippled portions.

with the elongation and narrowing of the spondylium in the Pentamerinæ in order to produce more surface for attachment of the diductor muscles. In the Gypidulinæ, where the spondylium has not been so pronouncedly narrowed, there are usually preserved well marked remnants of the interareas. This is particularly true of *Sieberella*.

Another feature of pentamerid shells in the vicinity of the beaks is the production of prominent flattened areas which greatly simulate an interarea. This feature is perhaps most strongly developed in *Brooksina* which has practically no interarea but has a broad flat region that extends from the beaks of both valves to the point of contact of the ribbed portions. These false cardinal areas are best developed in that genus and in *Capelliniella*, both groups having the convexity of the valves reversed from the normal, and there may be some mechanical connection between the two phenomena.

VENTRAL INTERIOR.—Important features of the ventral valve are the delthyrium and its accessories, the

deltidial cover and deltidial plates, and the spondylium and its supporting septum.

1. *Delthyrium*.—So far as our observations have extended, the delthyrium of the Camerellidæ is open except for marginal thickenings along the delthyrial border, alluded to below. No deltidial cover such as occurs in *Conchidium* has been seen.

2. *Deltidial cover*.—In *Conchidium* there is a truly remarkable cover to the delthyrium which we hesitate to call a deltidium, preferring the more non-committal term deltidial cover. As commonly described, this has been termed a "concave deltidium." Our investigations show that this structure is concave toward the anterior portion of the delthyrium, but when followed to the vicinity of the beak it rises above the margins of the delthyrium and projects dorsally in the form of a sheath with rather rectangular sides and depressed center. A similar structure exists in one specimen of *Harpidium*, but was erroneously described as convex deltidial plates. These two occurrences are the only ones noted by us in which there is a cover plate over the delthyrium. A concave "deltidium," presumably like the above, has been reported in *Pentamerus* but we have not seen such. The structure in *Conchidium* appears to be a pedicle sheath; it is not known definitely whether it had an open foramen at the apex, but it appears to have had one. In the specimen of *Harpidium* preserving the deltidial cover the beak is crushed down on the cover so that its precise structure can not be determined. Parenthetically it may be added that among the orthids and strophomenids no such cover as this has been observed.

3. *Deltidial plates*.—Hall and Clarke announced the presence of deltidial plates in several genera studied by them and even went so far as to use these structures as one of the generic distinctions between *Gypidula* and *Sieberella*. The present writers have not observed in any of the pentamerids that have come under their observation any clearly developed, typical deltidial plates. We have seen thickenings along the delthyrial margins of many of the genera, and such structures as these were termed "pseudo-deltidial plates" by Booker.³ These thickenings, in our experience, never restrict the delthyrium in any notable degree, certainly not nearly so noticeably as do similar thickenings in *Glossorthis*, *Hesperorthis*, and other orthid genera. Similar structures were observed also in specimens of *Conchidium* that have the deltidial cover as well. It therefore appears to us that they are of little taxonomic significance, certainly not sufficiently important to warrant the removal of the Pentameracea (restricted) to the Telotre mata, as Kozłowski has done.

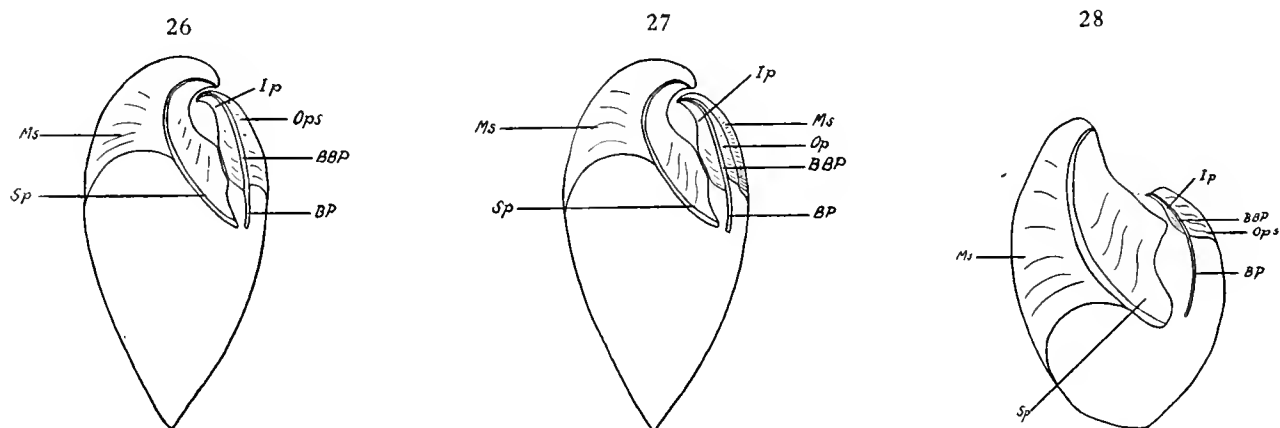
³ Booker, Jour. Proc. Roy. Soc. N. S. Wales, vol. 60, 1927, p. 134.

4. *Spondylium*.—The spondylium is an important feature of the pentamerids. It is always of the duplex type as described by Kozłowski, in which the septum is composed of two closely apposed pieces.

One tendency among the pentamerids, achieved in only two instances, is the reduction of the septum and the elongation of the spondylium. In extremely ventricose forms the rostral chamber is elongated and narrowed, so much so in some species that the sides are only a couple of millimeters apart. This elongation and narrowing of the spondylium is evidently for greater surficial spreading of the diductor muscles, permitting a strong pull without a breaking strain on the sides of the muscle platform.

4. Supporting plates consist of two subparallel septa extending from the middle of the valve and uniting with the inner, convex surfaces of the alar processes. It is clear that the function of these plates is to support and make rigid the rest of the cardinalia. In *Camerella* the supporting plates converge inward and unite with a septum.

Musculature.—Of great interest among the Camerellidæ is the position of the dorsal adductor scars in front of the cruralium in *Camerella* and forward of the parallel plates in *Parastrophinella* and *Anastrophia*. This is very different from the situation of the same muscles in the Pentameridæ, in which they are located



FIGS. 26-28.—Longitudinal sections of pentamerids. 26, *Pentamerus*; 27, *Pentameroides*; 28, *Conchidium* s. s. BP, brachial process; BBP, base of same; Ip, inner plate; Ms, median septum; Op, outer plate; Ops, outer plate and septum; Sp, spondylium.

DORSAL INTERIOR. Septa.—The dorsal interior of the Camerellidæ is fundamentally different from that of the Pentameridæ and will be treated first. Here the dorsal septa can be divided into four more or less distinct parts: (1) the brachial supports, (2) the alar processes, (3) the fulcral plates, and (4) the supporting lamellæ.

1. The brachial supports appear to be extensions from the postero-ventral extremity of the alar processes. They are blunt and short, and are defined by ridges along the posterior margin of the alar plates.

2. The alar processes appear as concave plates, convex inward, which define the walls of the notothyrial cavity at the posterior. These processes in their forward extension curve outward. The alar extensions may represent the complete supports of the lophophore, taking the place of the elongate processes in other forms.

3. Fulcral plates are small plates, concave dorsally, which define the sockets much as in the Orthoidea (Plectorthidæ and Schizophoriidæ).

within the confines of the subparallel or divergent septa or within the subrostral vault of the cruralium. In the Camerellidæ the situation of the adductors is much like that of the adductors in the Syntrophidæ and Huenellidæ, and it is very likely that future study will show the origin of the Camerellidæ out of these groups. This supposition, however, must await the discovery of the pallial marks in the Camerellidæ and will be decided by the course of these structures on the inner surface of the dorsal valve.

As stated above, the muscle-scars of the Pentameridæ are borne within the septal plates of the dorsal valve, and in the spondylium of the opposing one. This enclosure of the dorsal muscles by the septa is held by us to be a markedly characteristic feature of the Pentameridæ, differentiating them from the Camerellidæ.

Cardinalia.—The cardinalia of the Pentameridæ are the most characteristic feature of the genera and probably of the family as well. These lamellæ are

divisible into four distinct units termed by Leidhold:⁴ (1) The inner crural plate, (2) the outer crural plate, (3) the crural band or border, (4) the septal plate. We prefer to term the first two of these parts simply the outer and inner plates, since we do not feel that it is at present certain that they are the homologues of the crura such as occur in the Rhynchonellacea and Terebratulacea.

1. The inner plates are curved, convex ventrally, and unite with the outer plates and the wall of the valve to form a prominent umbonal chamber. The sockets into which the ventral teeth fit are notches in the inner plates where they unite with the wall of the valve. The designation "inner plates" is not entirely apt, since, when the valves are seen in ventral view, the plates are actually the outermost part of the cardinalia. Leidhold evidently coined his expressions from a specimen that had been split longitudinally (this at least is the way he figures the structures). Thus seen from the side, the plates are innermost, being next to the spondylium.

2. The outer plates are rather thin and low, and unite with the dorsal edge of the inner plates and are separated from the septal or supporting plates by (3) a band or longitudinal thickening, the "Cruralleiste" of Leidhold.

4. The septal or supporting plates unite with the floor of the valve or with each other if a cruralium is present, and they support the other structures. They are commonly rather long and may be the best developed of the tripartite cardinalia.

Further discussion is necessary regarding the *Cruralleiste* or base of the brachial support as we prefer to term it. This band is prolonged into a free process that commonly extends to the front end of the ventral spondylium. It is this elongate, free process that undoubtedly was the support of the lophophore. The *Cruralleiste* represents the growth path of this brachial support or rather the remnant of the brachial support which has been enclosed and encroached upon during the forward growth of the inner and outer plates. These brachial processes are rather stout in the Gypidulinæ but in some members of the Pentamerinæ are long and slender. In *Brooksina*, with its strongly arched valve, the processes are exceedingly long.

The cardinalia of the Pentameridæ as herein described are absolutely distinctive, nothing like them being known elsewhere. There is a slight difference between the septa of the Gypidulinæ and the Pentamerinæ. That of the former is commonly bowed or convex outward, especially where the inner and outer plates unite with the base of the brachial support. This is notably true of *Gypidula*, *Sieberella*, and *Pentamerella*. In the Pentamerinæ, on the other hand, the plates are generally higher and consequently not notably bowed.

GENERIC AND EVOLUTIONARY TRENDS

The following discussion points out the more important generic and evolutionary trends among the pentamerids observed by us, and indicates as well what characters we regard as of most import in defining the genera.

LOSS OF INTERAREAS AND DEVELOPMENT OF A PLANAREA.—In all of the pentamerids the inherited interareas are reduced to mere remnants and in many of the genera they have totally disappeared. But along with their vanishing comes the development in a few stocks of planareas or so-called false areas, plane (or nearly so) surfaces developed on either side of the delthyrium and largest in *Brooksina*. This development of planareas is of little taxonomic significance so far as present knowledge goes. The great reduction of the interareas is of course characteristic of the whole superfamily.

ROSTRATION.—Elongation of the beaks is best developed in *Conchidium*, *Harpidium*, and *Lissocœlina*, and along with this extreme rostration has come a great arching of the ventral beaks over the dorsal ones.

REVERSION OF NORMAL CONVEXITY.—This is a common tendency among many brachiopod stocks and the cause of it is not fully understood. In *Strophomena* of the Strophomenacea it has been correlated by Sardeson⁵ with a pendant growth habit, but this gravity causation does not appear to be responsible for the reversion in *Brooksina* and *Capelliniella*.

Reversion of fold and sulcus is another common feature, and one that is not uncommonly attended by rather profound alterations of the interior, and yet *Pentamerella* and *Sieberella* are structurally alike internally though the fold and sulcus are reversed. In *Virgiana*, Twenhofel⁶ says that the reversion of fold and sulcus takes place during growth, hence he regards it as a generic character, but to us this is certainly not so important as the internal features.

TRILOBATION.—The flattened pentamerids such as *Pentamerus* and *Rhipidium* developed pronounced trilobation, which may be tied up with their incurrent and excurrent canals as explained in the Orthidæ. This trilobation is also exhibited in the galeate pentamerids and the Camerellidæ by the development of a fold and sulcus.

ORNAMENTATION.—It appears clear that the first of the known Camerellidæ were practically smooth during early growth and that later the stock became more and more costate. Among the Gypidulinæ the first members to appear, *Clorinda* and *Barrandella*, were smooth, and were followed by costate genera.

⁴ Abhandl. preuss. geol. Landesanst., n. ser., Heft 109, 1928, pp. 51-53.

⁵ Pan-Amer. Geol., vol. 51, 1929, pp. 37-38.

⁶ Geol. Surv. Canada, Mus. Bull. 3, 1914, pp. 27-28.

Gypidula becomes secondarily smooth or nearly so in the late Devonian. On the other hand, smooth *Gypidula pseudogaleata* may represent a totally different stock generically from any of the others.

The first of the known American Pentamerinæ are the costate *Platyerella* and *Virgiana*. They were followed by smooth forms (*Pentamerus*, *Pentameroides*, etc.), and these were later succeeded by *Conchidium* and allies. The strongly costate forms are certainly characteristic of the high Middle and Upper Silurian, especially of central United States and Alaska.

LOSS OF THE VENTRAL SEPTUM.—Many pentamerids eliminate more or less of the ventral septum. Complete loss was nearly achieved by *Pentamerella* and some species of *Gypidula*, and total loss of the septum is the case in *Cymbidium* and *Holorhynchus*. On the other hand, *Platyerella* and *Virgiana*, earliest of the Pentamerinæ, had exceedingly short dorsal septa, and some later stocks had longer ones.

DEVELOPMENT OF A CRURALIUM.—Among the galeate Pentamerinæ *Sieberella* and *Barrandella* alone have cruralia. In the Pentameridæ the genus *Pentameroides* is the only one known to have this structure. *Conchidium* with a cruralium is theoretically possible, but so far none is known.

PARALLEL TRENDS

A number of interesting parallel developments were seen during this study in various groups of the pentamerids. One of these is in the development of a cruralium. *Camerella* has a cruralium in the dorsal valve but its homœomorph, *Parastrophinella*, has the dorsal septa separate. In *Barrandella* there is a cruralium but in *Clorinda*, its homœomorph, the dorsal plates are widely separate. The same is true of *Pentamerus* and *Pentameroides*, and of *Sieberella* and *Gypidula*. Hall and Clarke⁷ regarded this development of a cruralium as of not more than specific value and placed more reliance on the external form of the shell. The trend of more recent times is, however, to take the opposite view, regarding the internal variations as of greater importance than the exterior. Accordingly we recognize the presence of a cruralium as of generic value.

SUMMARY

In summarizing the above remarks, we can not survey the evolution of the pentamerids in any clearer way than by showing our conceptions of the interrelations of the various members of the Pentamerinæ.

The subfamily, on the basis of external characters, is at once separable into two divisions, Læves and Costatæ, with the following arrangement in equivalent states of development:

| Smooth | Costate |
|----------------------|---|
| <i>Pentamerus</i> | <i>Platyerella</i> , <i>Rhipidium</i> |
| <i>Pentameroides</i> | None as yet known |
| <i>Lissocœlina</i> | <i>Conchidium</i> |
| <i>Capelliniella</i> | <i>Brooksina</i> |
| <i>Holorhynchus</i> | <i>Cymbidium</i> |
| <i>Harpidium</i> | None known, but to be looked for in <i>Conchidium</i> with abbreviated septum |

We do not mean to say that these two groups represent two genetic lines. This is possible, but as yet we do not know pentamerids well enough to state it as a fact. There are too many possibilities in the way of smooth stocks becoming costate and costate stocks going back into the smooth state. However, our scheme is interesting, even if not established. It will be noticed that out of the six possibilities, four of the smooth stocks have a costate genus in a corresponding stage of development.

Family CAMERELLIDÆ Hall and Clarke 1894

(Syn. Parastrophininæ Schuchert 1929)

Primitive, small, usually multicostate Pentameracea with the dorsal shell the deeper and with small, narrow ventral interareas; probably derived out of the Syntrophiidæ. All have a spondylium duplex. Dorsal cardinalia tripartite, with the septal plates either discrete or united into a cruralium supported by a median septum; arm supports short. Adductor muscles attached to the floor of the dorsal valve in front of the septal plates. Delthyrium open and but rarely modified by narrow delthyrial marginal growths.

Embraces the following genera:

Camerella Billings
? *Branconia* Gagel
Parastrophinella Schuchert and Cooper
Anastrophia Hall
Metacamerella Reed

The genetic relations appear to be as shown in Table 18.

⁷ Pal. N. Y., vol. 8, pt. 2, p. 246.

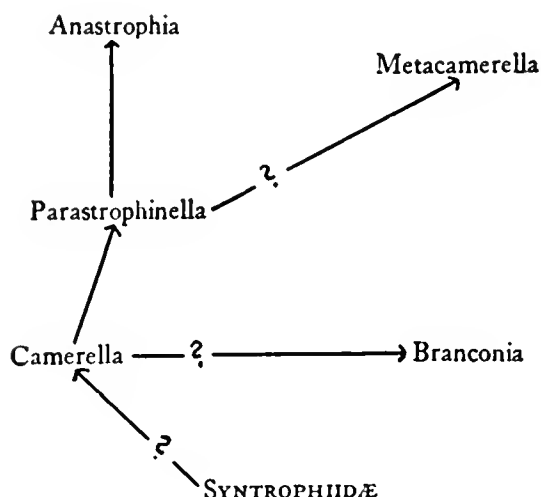
DISCUSSION.—Hall and Clarke say:⁸

Whatever may be the oscillation in form and the variation in secondary characters presented by *Camarella*, *Parastrophia* and their allies, present evidence indicates that they must be regarded as the genetic precursors, as they are the secular precedents of the great group of true pentameroids.

And on page 355 they erect the family Camerellidæ for *Camarella*, *Parastrophia*, *Anastrophia*, and ? *Branconia*; all the other genera referred here by them are now excluded from this family.

Table 18

CAMERELLIDÆ



Beecher and Clarke⁹ have shown

that in early age the shells of *Anastrophia* are normally biconvex, and the brachial valve scarcely deeper than the opposite. . . . In this condition the form of the shell resembles that of normal individuals of *Camarella volborthi*, and in this series of forms, beginning in *Camarella* where senile shells evince a gibbosity of the brachial valve and a tendency toward reversion of convexity, and ending with the Lower Helderberg *Anastrophia verneuili*, we have a consecutive and gradational development in internal structure, which is accompanied by more abrupt variations in exterior.¹⁰

As conceived by the present writers, the Camerellidæ consist of shells in which the dorsal valve is usually more convex than the ventral. The shells are commonly multicostate. The ventral interior has a prominent spondylium duplex, but the most important family

characters are in the dorsal valve in connection with the cardinalia. The brachial processes are supported by alate plates, concave outward, and these are, in turn, supported by septal plates which are either discrete and fastened directly to the floor of the valve as in *Parastrophinella* and *Anastrophia*, or converge and unite with a median septum to form a cruralium as in *Camarella*. Another feature of significance is the attachment of the adductor muscles to the floor of the dorsal valve entirely outside the septal plates. This is a more primitive feature than in the derived Pentameridæ, in which the adductor muscles are confined either within or on the dorsal septal plates or cruralium when such a structure is present.

The family as now constituted contains one genus, *Branconia*, which is of doubtful value, and another, *Metacamerella*, which has not been adequately described. The former, which occurs in the Middle Ordovician of Europe, is probably identical with *Camarella*. *Metacamerella*, on the other hand, suggests an *Anastrophia*, having a ventral fold, but the alate processes of the dorsal valve were not reported by the nomenclator of the genus.

In the Camerellidæ the delthyrium appears to be open or partially encroached upon by marginal growths which have been called deltidial plates, but they are not like those in the Telotremata and it appears probable that true deltidial plates do not occur in this family.

Genus CAMERELLA Billings 1859

Pl. 25, figs. 3-6, 8-13, 16, 20-22, 24, 27-30, 43

Billings, Canadian Nat., vol. 4, 1859, p. 301.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, p. 219, pl. 62, figs. 11-18 (*Camarella*).

Hom. *Parastrophia* Hall and Clarke, Ibid., p. 221, pl. 63, figs. 1-3.

Syn. *Parastrophina* Schuchert and LeVene 1929.

GENOLECTOTYPE (Hall and Clarke).—*C. volborthi* Billings 1859.

DESCRIPTION. *Exterior*.—Subglobular to subpentagonal in outline; hinge-line narrow, cardinal extremities broadly rounded; profile unequally biconvex, the dorsal valve having the greater convexity in mature individuals; anterior commissure uniplicate. Ventral interarea narrow, nearly obsolete; delthyrium open, so far as known. Dorsal interarea obsolete. Surface costate on the anterior half, smooth posteriorly. Shell substance fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth strong; dental and septal plates convergent to form a spondylium duplex. Septal plates in conjunction and prolonged in front of the spondylium for some distance.

Dorsal interior.—Notothyrial cavity deep and elongate; brachial supports rather short and blunt; septal plates, which buttress the brachial support, elongate

⁸ Pal. N. Y., vol. 8, pt. 2, p. 341.

⁹ N. Y. State Mus., Mem. 1, 1889, p. 32.

¹⁰ Hall and Clarke, op. cit., p. 225.

and convergent, forming a cruralium duplex; short alæ present just anterior to the brachial supports.

GEOLOGIC RANGE.—Middle Ordovician (Chazy) to Middle Silurian of North America.

SPECIES

Camerella n. sp.

C. volborthi Billings 1859

Parastrophia greenei (Hall and Clarke) 1895 (placed here after a study of Hall and Clarke's figure)

P. hemiplicata (Hall) 1847

P. hemiplicata rotunda (Winchell and Schuchert) 1893

P. rotundiformis Willard 1928

P. ? scofieldi (Winchell and Schuchert) 1893

DISTINGUISHING CHARACTERS.—*Camerella* as here restricted is characterized by the presence of a spondylium duplex, a cruralium duplex, and dorsal septa having short alate extensions on the outside.

DISCUSSION.—The genotype selected by Hall and Clarke is *C. volborthi* Billings, which proves to be structurally identical with *Parastrophia hemiplicata* Hall, the type species of that genus. Both forms have the same kind of spondylium and cruralium and possess the alæ which are so much better developed in *Anastrophia*. It is evident, then, that *Parastrophia* Hall and Clarke 1893 (a homonym replaced by *Parastrophina* Schuchert and LeVene 1929) and *Camerella* Billings 1859 are synonyms, and the latter name has priority.

Regarding *Camerella*, Hall and Clarke say that these shells have "in effect, a rhynchonelloid exterior," with a well defined spondylium supported by a short median septum, and an open delthyrium without deltidial plates. The cardinalia consist of "crural plates converging and forming a short, very small median cavity, which is supported by a long septum," and this hinge structure "is similar to that of *Camarotoechia* . . . The crura are short, and the lateral divisions of the hinge-plate small. No cardinal process exists. The internal structure of *Camerella* is, thus, not unlike that of *Syntrophia*, notwithstanding the wide difference of exterior."

It is evident that there is needed a revision of the species commonly referred to *Camerella* under the current conception of the genus.¹¹ The present writers exclude from this genus *C. bella* Fenton, *C. ambigua* (Hall), *C. inornata* Weller, and the following species of Billings: *C. varians*, *C. longirostris*, *C. panderi*, *C. costata*, *C. polita*, and *C. parva*. Some of these

species must be removed to entirely different groups. *C. inornata* Weller does not have the external form of either *Camerella* or *Rhynchocamara* and should probably be assigned to ? *Cyclospira*. "*Camerella*" *panderi* appears from etched specimens to possess spiralia and is without a spondylium, as is also *C. longirostris*. "*Camerella*" *ottawacensis* from Paquette Rapids (pl. 16, figs. 6, 9, 13) apparently belongs to *Orthorhynchula*.

In *Camerella* the ventral muscles are confined to the spondylium as is normal for spondylium-bearing shells, but in the dorsal valve internal molds show clearly four adductor impressions bisected by the septum of the cruralium. This must be regarded as a primitive character and is in contrast to the Pentameridae in which the muscles are enclosed by the septal plates or are confined to the cruralium. In the Camerellidae the cruralium is the base of attachment of the diductor muscles.

Genus BRANCONIA Gagel 1890

(Compare with *Camerella*)

Gagel, Beitr. z. Naturkunde Preuss. hrgb. von d. Physik.-Oekonom. Gesell. z. Königsberg, vol. 6, 1890, p. 62, pl. 4, fig. 12.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, p. 223.

GENOHOLOTYPE.—*B. borussica* Gagel 1890.

DESCRIPTION (translation from Gagel).—Outline transversely lengthened, ventral valve (? dorsal) strongly arched, provided with a thick, keel-like elevated fold, which is divided in the middle by a low, but definite groove. On the anterior margin the ventral (dorsal ?) valve is provided with a deep indentation; the beak is small but so strongly incurved that it touches the dorsal valve and no foramen can be perceived. Hinge margin somewhat narrower than the greatest shell width, slightly curved. Dorsal valve (? ventral) flattened, with a small beak, from each side of which there runs a small flat surface that joins with the shell proper at an angle. Close under the beak begins a very deep, steep sinus; at the anterior margin the dorsal valve is drawn out into a rather noticeable tongue which is bent gradually toward the remaining valve at a right angle; the tongue fills up the indentation of the anterior margin of the ventral (? dorsal) valve. Unfortunately this part of the anterior margin is quite damaged, so that the exact outline can no longer be ascertained. The outer shell layer is preserved in a few places only, and shows a very fine, concentric ornamentation. Both valves are distinguished by the possession of a very large, strong, median septum which extends from the beak to half the length of the shell. Aside from these septa, which are clearly visible on the outer surface of the shell, nothing is known of the interior.

DISCUSSION.—Gagel thought *Branconia* was a rhynchonellid but found that it agreed with no known

¹¹ For the early Middle Ordovician (Chazy) shells which have usually been called *Camerella*, but which have a different internal structure, we proposed the name *Rhynchocamara* in our "Synopsis" of 1931, and left the genus under the family Camerellidae. We are now convinced that it is in reality a rhynchonellid. For the convenience of workers on that group its description is amplified in the Appendix to this work.

genus. It does not belong to *Rhynchonella* or *Camerophoria*, since the sinus is situated on the dorsal (? ventral) valve; moreover, from *Rhynchonella* as well as from *Eatonia* and *Pentamerus* it is clearly differentiated in having a very large strong septum in each valve. The only existing example was found in a "Lower Silurian" (Ordovician) erratic boulder thought to belong to the Jewe horizon of the Estonian Ordovician.

Hall and Clarke remark on the fact that the author may have reversed the position of the ventral and dorsal valves. The presence of a septum in each valve and the occurrence of the shell in rocks of probable Trenton age suggests a relationship of *Branconia* to *Camerella*. However, in the absence of definite information regarding the nature of the interior and in the absence of comparative material, the genus will stand for the present.

Genus PARASTROPHINELLA Schuchert and Cooper 1931

Pl. 25, figs. 23, 25, 26; pl. 29, fig. 7

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 248.

GENOHOLOTYPE.—*Pentamerus reversus* Billings 1857, Geol. Surv. Canada, Rept. Prog. for 1856, p. 295; Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, pl. 63, fig. 11.

DESCRIPTION. *Exterior.*—Shell subglobular in outline, hinge-line narrow, lateral profile biconvex, the dorsal valve always the more convex and usually arched somewhat over the ventral interarea. Anterior commissure broadly uniplicate. Ventral interarea narrow, apsacline, beak curved slightly, delthyrium open, so far as known. Dorsal interarea obsolete, beak incurved, umbo strongly arched. Surface costate, the costæ being faint or obsolete at the umbones as in *Camerella*. Shell structure fibrous, impunctate.

Ventral interior.—Like that of *Camerella*, with a prominent spondylium duplex, the septal plates of which are prolonged for some distance in front of the spondylium. In one species and in some individuals of other species the spondylium is sessile at the posterior of the shell.

Dorsal interior.—Like that of *Anastrophia*, with the septal plates discrete or convergent only at their front ends. Alæ somewhat better developed than in *Camerella*. Adductor scars anterior to the cruralium.

GEOLOGIC RANGE.—Upper Ordovician to Middle Silurian of North America.

SPECIES

- Parastrophia divergens* Hall and Clarke 1895
- P. latiplicata* Hall and Clarke 1895
- P. multiplicata* Hall and Clarke 1895
- P. ops* (Billings) 1862
- P. reversa* (Billings) 1857

DISTINGUISHING CHARACTERS.—This new genus differs from *Camerella sensu stricto* chiefly in the divergence of the septa of the dorsal valve, which do not form a cruralium duplex. It thus forms, with the other Camerellidæ, a parallel series with the Gypidulinæ.

DISCUSSION.—Hall and Clarke proposed the name *Parastrophia* and typified the genus by *Atrypa hemiplicata* Hall. Little did they realize that they had selected a genotype whose internal structure is identical with that of *Camerella volborthi* Billings. However, several of the later species usually placed under the old name of *Parastrophia* prove to have features in the dorsal valve differing from those of *Camerella* and are here placed under the new name *Parastrophinella*, chosen to preserve a semblance of the old term.

It is known from internal molds that the adductor muscles of the dorsal valve of *Parastrophinella* were situated entirely outside of the cruralium as in *Camerella*. In this respect, *Parastrophinella* agrees with the other members of the family.

Genus ANASTROPHIA Hall 1867

Pl. 25, figs. 14, 15, 19, 33-36, 38-42

Hall, N. Y. State Cab., 20th Rept., 1867, p. 163.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, p. 224, pl. 63, figs. 31-38.

Hom. *Brachymerus* Shaler 1865

GENOLECTOTYPE (Hall and Clarke).—*Pentamerus verneuili* Hall 1857, N. Y. State Cab., 10th Rept., p. 104, figs. 1, 2.

DESCRIPTION. *Exterior.*—Globular to subelliptical; hinge-line straight, narrow; cardinal extremities broadly rounded; lateral profile unequally biconvex, anterior commissure uniplicate, the dorsal fold usually being defined only in the anterior half of the valve. Ventral interarea small and narrow, cleft by an open delthyrium; dorsal interarea obsolete; beak curved, commonly resorbed. Surface multicostate; shell substance fibrous, impunctate.

Ventral interior.—Teeth narrow, sharp, with deep crural fossettes, the teeth forming a strengthening ridge along the delthyrial margin; dental plates convergent, making with the septal plates a spondylium duplex which is sessile or nearly so at the posterior of the shell and is supported in front by the median septum. Scar of pedicle attachment located just beneath the dental ridges.

Dorsal interior.—Notothyrial cavity deep; brachial supports stout curved processes, carinate on their posterior face, sloping laterally into a concave fulcral plate which is attached to the inner shell wall. Sockets deep. Septal plates nearly vertical lamellæ, subparallel or converging slightly toward the anterior. On the outside of these plates and beneath the brachial supports are winglike plates which are concave outward. In the

middle of the space between the septal plates is a low ridge with diductor scars on each side which probably served as a cardinal process. The adductor impressions are four in number, a posterior pair located on the outside of the anterior ends of the septal plates, and a larger anterior pair that is elongate or sub-trigonal in outline.

GEOLOGIC RANGE.—Middle Silurian to Lower Devonian.

AMERICAN SPECIES

Anastrophia brevirostris (Hall) 1852
A. internascens Hall 1879
A. interplicata (Hall) 1852
A. verneuili (Hall) 1857

EUROPEAN SPECIES

Anastrophia deflexa (Sowerby) 1839
A. magnifica Kozłowski 1927

DISTINGUISHING CHARACTERS.—*Anastrophia* is distinguished from *Parastrophinella* chiefly by the more completely costate exterior.

DISCUSSION.—There is some variation in the spondylium of *Anastrophia*. In some specimens it is supported for its whole length by the ventral septal plates, but in others the posterior end rests on the floor of the valve. In one unique individual (pl. 25, fig. 42) the walls of the spondylium have bent inward and united, forming a tubular chamber open at the front and back. Such a structure must have impaired the activity of the muscles and is regarded as a pathologic case. In many of the specimens the scar of the pedicle attachment is to be seen in a depression on each side of the spondylium just beneath the tooth ridges. The ventral beak and the dorsal umbo as well are commonly more or less abraded by the pedicle.

The cardinalia of the dorsal valve are typical of the family. There are long brachial supports and outside of these are broad, alate expansions. The posterior ends of the septal plates unite with the inner surfaces of the alæ, which are carinate, thickened in the back, and slope off on the outside to unite with a thick, concave plate that serves as a socket. Adductor scars are visible at the front ends of the septal plates, not having become enclosed as in the Pentamerinæ.

Genus METACAMERELLA Reed 1917

Reed, Trans. Roy. Soc. Edinburgh, vol. 51, art. 4, 1917, p. 934, pl. 23, figs. 14-18.

GENOHOLOTYPE.—*Stricklandia* ? *balclatchiensis* (*balclatchiensis*) Davidson 1883, Brit. Foss. Brach., vol. 5, Sil. Suppl., p. 166, pl. 9, figs. 27-29.

ORIGINAL DESCRIPTION.—Shell oval, biconvex. Pedicle-valve with low median fold near anterior end composed of

several longitudinal plications chiefly developed towards front end; beak high, incurved, with open delthyrium; small false area on each side; interior with small subumbonal spondylium and short median septum. Brachial valve with lower beak than opposite valve; low median fold near anterior end, composed of several longitudinal plications; interior with pair of long recurved crura, pair of long parallel median septa, and muscle-scars as in *Parastrophia*. Shell thick, fibrous, punctate externally.

DISCUSSION.—In the absence of material, Reed's genus is difficult to place in our taxonomic scheme. From the morphology as described by him, it is evident that *Metacamerella* is very close to *Parastrophinella* and to *Anastrophia*. It differs from the former externally in possessing a fold on both valves. Unfortunately Reed's illustrations do not adequately bear out this statement, as figure 18, of the dorsal valve, shows a decided sulcus and appears to be a totally different shell from the one under consideration. Figures 15 and 17, however, clearly have a fold. According to Reed, the muscle marks of the dorsal valve are like those of *Camerella* (*Parastrophia*), but the figures again, except for figure 18, do not show them. Should figures 14 and 18 represent opposite valves, the genus would not be difficult to place and we could say at once that it is structurally a *Parastrophinella* with fold and sulcus reversed, and clearly belongs in association with *Anastrophia* and *Camerella*.

The question of punctation among pentamerids is a very important one. Reed states that the punctation is external, and we have shown in our discussion of orthids that exopunctæ have no taxonomic significance beyond genera. This is best seen in *Porambonites* and *Linoporella*, genera that have developed the same kind of exterior, but the former has an impunctate shell and the latter is endopunctate as in the Dalmanellacea. From the internal characters of *Metacamerella* it would appear to be impunctate as are all other pentamerids.

From the above discussion it seems best to place *Metacamerella* close to *Anastrophia*, the chief known generic difference of the former being a fold on the ventral valve. Were it not for Reed's assertion that *Metacamerella* possessed a dorsal fold, which seems unlikely, to judge by the ventral valve he figures, we would exclude from his genus his figures 15 and 17.

Family PENTAMERIDÆ McCoy 1844, emend.

Terminal, usually rostrate Pentameracea, probably derived out of the Camerellidæ. Shells smooth, costate or multicostate. Ventral interareas short and narrow, but often obsolete, or plane areas are developed. In nearly all there is a more or less large spondylium

duplex, supported by either very long or short double septa; but in two genera the spondylium hangs free. Dorsal cardinalia—the most characteristic feature of the family—tripartite; consisting of discrete plates, or united into a cruralium that bears the adductor muscles. When the plates are discrete, the adductors are on the floor of the shell between them. Brachial processes very long, and in some forms terminally divergent. A cardinal process is usually absent or, when present, is a rudimentary septum or a low callosity. A concave deltidium and incipient deltidial plates are sporadically developed, but in general the delthyrium is open. Shell substance fibrous, impunctate.

GEOLOGIC RANGE.—Silurian and Devonian.

Embraces two subfamilies: Gypidulinæ Schuchert and Pentamerinæ Waagen.

DISCUSSION.—The Camerophoriinæ of the Devonian and Carboniferous, long included in the Pentameracea, are now considered to be spondylia-bearers of the Rhynchonellacea, and the Porambonitidæ are in the present work shown to be much modified Orthacea.

Subfamily GYPIDULINÆ Schuchert 1929

Pentameridæ more or less galeatiform, with small ventral interareas. Ventral valve always the more convex and deeper. Cardinal process simple, but usually absent. Shells smooth, or with some low or many rounded costæ.

GEOLOGIC RANGE.—Silurian and Devonian.

Includes the following genera:¹²

Clorinda Barrande (syn. *Barrandina* Booker 1926)

Barrandella Hall and Clarke

Gypidula Hall

Sieberella Oehlert

Pentamerella Hall

? *Zdimir* Barrande

The genetic relations are about as shown in Table 19.

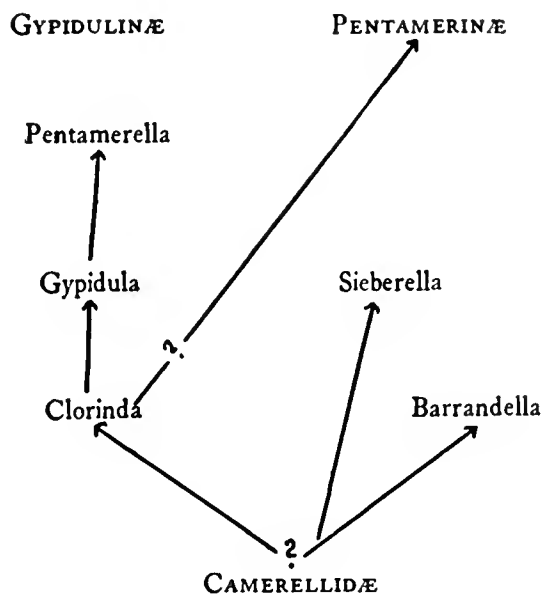
DISCUSSION.—We include in the subfamily Gypidulinæ all of the galeatiform Pentameridæ having the internal structure of the family. This subfamily was rather prominent in the Silurian and Devonian but evidently did not survive the latter period. As previously constituted, it included *Virgiana*, but the structure of the dorsal septal plates in the latter genus is so close to that in *Pentamerus* that it must be referred to the Pentamerinæ. Its previous constant association with the Gypidulinæ is undoubtedly due to the erroneous figure of the interior published by Hall and Clarke.

¹² Our genus *Liocælia*, which was included in this subfamily in 1931, is now seen to be a rhynchonellid; it is further described in the Appendix to this work.

Clorinda and *Barrandella* show some internal variations from the rest of the subfamily. At the junction of the inner and outer septal plates of the dorsal valve there is a small process extending in a ventral direction and into the notothyrial chamber. This feature has not been observed in *Gypidula*, *Sieberella*, or *Pentamerella*, but was noticed in one specimen of *Clorinda*.

In the Gypidulinæ occur some interesting parallelisms. *Barrandella* and *Clorinda* are externally alike but in the former the plates of the dorsal valve form a

Table 19



cruralium whereas in the latter they are discrete. The same relations also hold for *Sieberella* and *Gypidula*. These striking features are not only of great interest but are of considerable importance to students of stratigraphy and paleogeography.

Genus CLORINDA Barrande 1879

Pl. 26, figs. 8-12, 21; t. fig. 29

Barrande, Syst. Sil. Bohême, vol. 5, 1879, p. 109, pl. 119, figs. 1-4.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, p. 244. Syn. *Barrandina* Booker 1926 (genotype, *B. wilkinsoni* Booker 1926 = *Pentamerus linguifera* var. *wilkinsoni* Etheridge 1892 (pars)), Jour. Proc. Roy. Soc. N. S. Wales, vol. 60, p. 131.

GENOHOLOTYPE.—*C. armata* Barrande 1879.

DESCRIPTION. *Exterior.*—Subgaleatiform; hinge-line straight, cardinal extremities broadly rounded; lateral profile biconvex, the ventral valve having the greater convexity. Anterior commissure uniplicate; ventral sulcus usually ill defined; anterior of ventral

valve produced into a long tongue; dorsal fold low, best defined at the front. Ventral interarea narrow and short, curved apsacline to orthocline, beak strongly curved, umbo inflated; dorsal interarea obsolete, beak curved, umbo swollen. Valves unornamented except by concentric lines of growth. Shell structure fibrous, impunctate.

Ventral interior.—Delthyrial cavity shallow; teeth small, dental and septal plates forming a small spondylium duplex, which is free at its anterior end.

Dorsal interior.—The septa of the dorsal valve are subparallel or divergent as in *Gypidula*. At the junction of the inner plates with the base of the brachial process there is a carina pointing ventrally. The brachial process is wide, moderately long.

GEOLOGIC RANGE.—Silurian of North America, Europe, and Australia.

and accordingly we feel that this carina has no significance in generic taxonomy. A plate of this kind was seen also in one specimen of *Conchidium*, and Booker shows them as well in *Gypidula galeata* from Gotland. We therefore hold that *Clorinda* is the smooth equivalent of *Gypidula*, having its fold on the dorsal valve. In this latter respect it differs from certain smooth *Gypidulas* (*G. pseudogaleata*) which may ultimately be referred to a new subdivision.

Booker has recently proposed a new genus *Barrandina* for shells having the external form of *Clorinda*, but thought to differ from the latter in the dorsal interior. He defines his genus in part as follows:

At the junction of the crural plates and septa a pair of curved, outwardly convex plates are developed. These are attached throughout their entire length to the cruralium, at the junction of the crural plates [inner plates] and septa

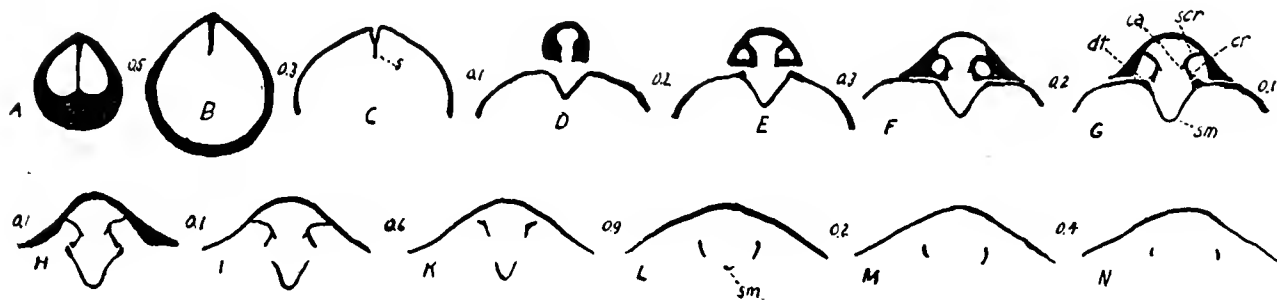


FIG. 29.—Serial sections of *Clorinda pseudolinguifera* Kozłowski. After Kozłowski. *ca*, carina at the limit of crural plates and crural septa; *cr*, crural plates (inner plates); *dt*, teeth; *scr*, crural septa (outer plates); *sm*, spondylium; *s*, septum.

AMERICAN SPECIES

Athyris (?) *tumidula* Billings 1866

EUROPEAN SPECIES

Clorinda ancillans Barrande 1879

C. armata Barrande 1879

C. bubo Barrande

C. pseudolinguifera Kozłowski 1929

DISTINGUISHING CHARACTERS.—*Clorinda* is a smooth shell, internally resembling *Gypidula*, and having the fold on the dorsal valve.

DISCUSSION.—Inside the ventral valve the septum is very short and the spondylium hangs free for most of its length. The dorsal cardinalia are like those of *Gypidula* and have rather long brachial processes as is typical of the family. The most notable distinction to be seen from *Gypidula* is the carina which runs along the base of the brachial process at its junction with the inner plate. In pentamerids of this type from Australia a carina may be seen also at the junction of the base of the brachial process with the outer plate,

[outer plates], either along the median line of the convex side of the plate, or at the edges, being then intercalated between the septa and crural plates. These plates extend beyond the anterior termination of the crural plates and septa for fully one-third of their length and terminate at a point slightly anterior to the end of the spondylium.

The sub-genus *Barrandina* has been erected for the reception of certain Australian Pentameridae, with the fold on the brachial valve and sinus on the pedicle valve, in which the cruralium is modified by the development of an extra plate at the junction of the septa and crural plates. The two species comprising the sub-genus were first described by Etheridge as *Pentamerus linguifera* var. *wilkinsoni*. Subsequent work on the pentameroids of the Yass district has revealed a series of forms paralleling in their structures the *Barrandella* and *Sieberella* series of Europe and America, but all characterized by the development of an extra plate in the cruralium.

It is our belief that the "extra plate" of Booker is actually the same as the brachial process of all other pentamerids but has more pronounced ridges than is usual along the junction of the inner and outer plates with the base of the brachial process. In our opinion the internal structure of *Barrandina* does not differ

generically from that of *Clorinda*. In *B. minor* Booker the septal plates are more widely divergent than in *B. wilkinsoni*, in which they are subparallel. The latter species is approaching *Barrandella*, but the former is quite a typical *Clorinda*. We therefore regard *Barrandina* as a synonym of *Clorinda*.

Genus BARRANDELLA Hall and Clarke 1893

Pl. 26, figs. 1-3, 5-7; t. fig. 30

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, pp. 241, 245, pl. 71, figs. 1-3, t. fig. 173; Handbook, pt. 2, 1895, p. 844, figs. 457-458.

GENOHOLOTYPE.—*Atrypa linguifera* Sowerby 1839, in Murchison, Sil. Syst., p. 629, pl. 13, fig. 8.

DISTINGUISHING CHARACTERS.—*Barrandella* is to

the genotype. Later Schuchert (1897) regarded it as a synonym of the older *Clorinda*. Recently the name has been revived by Booker (1926) and Kozłowski (1929), the latter recognizing *Barrandella* as a genus and *Clorinda* as a subgenus, but we prefer to regard both groups as of generic rank.

GEOLOGIC RANGE.—Silurian of North America and Europe.

AMERICAN SPECIES

Clorinda ventricosa (Hall) 1860

? *C. fornicata* (Hall) 1852

EUROPEAN SPECIES

Barrandella linguifera (Sowerby) 1839

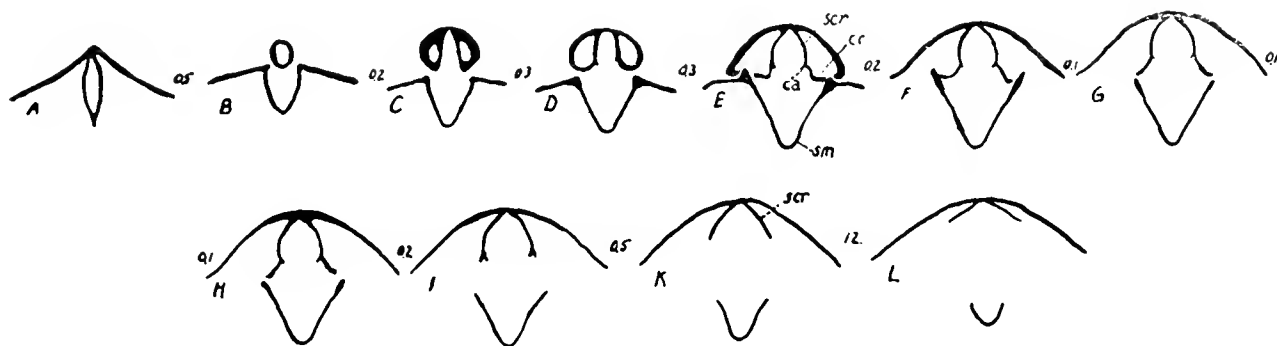


FIG. 30.—Serial sections of *Barrandella linguifera* (Sow.), from the Gotlandian of Dudley, England. After Kozłowski. *cr*, crural plates (inner plates); *ca*, carina at limit of crural plates and crural septa; *scr*, crural septa (outer plates); *sm*, spondylium.

be used for shells having an exterior and a ventral interior like those of *Clorinda*. Inside the dorsal valve, however, the supporting septa of the crural plates are convergent and unite to form a sessile or nearly sessile cruralium. On the outside of the dorsal valve, when the shell is worn, a single septum is visible, which is the track of the united plates.

A peculiar internal character of *Barrandella*, according to Hall and Clarke,

is the series of strong vascular [pallial], or ovarian sinuses, which radiate from the umbonal region of the pedicle-valve. These are complicated with the undefined diductor scars, and are therefore to a certain extent of muscular origin. In *Pentamerus fornicatus* these are highly developed and produce strong ridges on the casts of the valve; while in *P. ventricosus* they are more numerous and much finer. . . . It was for similarly ridged internal casts that Barrande proposed the generic term *Clorinda* (p. 244).

DISCUSSION.—Hall and Clarke proposed the name *Barrandella* with *Pentamerus linguifera* (Sowerby) as

Genus GYPIDULA Hall 1867

Pl. 26, figs. 18, 22-24, 26-29, 31, 32, 34-40

Hall, N. Y. State Cab., 20th Rept., 1867, p. 163.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, pp. 241, 247, pl. 72, figs. 15-24, t. fig. 177 (*comis*).

GENOLECTOTYPE (Hall and Clarke).—*Pentamerus occidentalis* Hall 1858, Geol. Surv. Iowa, vol. 1, pt. 2, p. 514, pl. 6, fig. 2 (*non P. occidentalis* Hall 1852); Belanski 1928, Univ. Iowa Studies, vol. 12, no. 7, p. 8.

DESCRIPTION. *Exterior.*—Galeatiform, hinge-line short and straight; cardinal extremities rounded; lateral profile biconvex, the ventral valve usually having the greater convexity. Anterior commissure rectimarginate or sulcate; the ventral fold usually low and defined at the anterior only. Ventral interarea very narrow, defined by low ridges, curved, apsacline to anacline, delthyrium large, open; beak pointed, incurved strongly; umbo inflated. Dorsal interarea ob-

solete; beak pointed, incurved; umbo swollen. Surface smooth or multicostate; shell substance fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; teeth strong, narrow, elongate; dental plates convergent, forming a narrow spondylium, supported by a duplex septum for part of its length; free at the front end. Septum short.

Dorsal interior.—Notothyrial cavity deep; crural apparatus consisting of three pairs of plates intimately united. At the posterior are two plates slightly convex inward, uniting with the postero-dorsal wall of the valve at the back and their dorsal or distal edges uniting with the brachial supports. These form a sort of hinge-plate. The sockets are excavations in the lateral edges at the junction with the wall of the valve. A second set of plates are set off from those above by ridges. These are vertical, narrow, elongate bands with their front ends free, and are supported by septa which converge inward and unite directly with the wall of the valve. Cardinal process simple, absent, or present in some species. The diductors are usually borne in a narrow pit under the beak. A low septum divides the space between the septal plates into two, and on each side of the ridge obscure adductor impressions are visible.

GEOLOGIC RANGE.—Silurian and Devonian of North America and Europe.

AMERICAN SPECIES

- Gypidula angulata* Weller 1903
G. coeymanensis Schuchert 1913
G. coeymanensis prognostica Maynard 1913
G. comis (Owen) 1852
G. cornuta Fenton and Fenton 1924
G. cornuta pareva Fenton and Fenton 1924
G. globulosa (Nettelroth) 1889
G. knotti (Nettelroth) 1889
G. laeviusculus Hall 1867
G. lotis (Walcott) 1884
G. mineolaensis Branson 1922
G. multicostata Dunbar 1920
G. nucleolata Belanski 1928
G. nucleus (Hall and Whitfield) 1875
G. occidentalis (Hall) 1858
G. papyracea Belanski 1928
G. pseudogaleata recurrens Meyer 1913
G. roemeri (Hall and Clarke) 1893
G. romingeri Hall and Clarke 1893
G. simplex Foerste 1909
G. subglobosa Maynard 1913
G. uniplicata (Nettelroth) 1889
 ? *G. pseudogaleata* (Hall) 1857

FOREIGN SPECIES

- Atrypa galeata* Dalman 1828
Gypidula dudleyensis Schuchert 1913
Pentamerus acutolobatus Sandberger 1850-1856

- P. acutolobatus procerula* Barrande 1879
P. caducus Barrande 1879
P. globus Schnur 1853
P. pelagica Barrande 1879 (in part)

DISTINGUISHING CHARACTERS.—*Gypidula* is most readily recognized externally by its galeate form and the position of the fold on the ventral valve. Internally the differential characters are in the dorsal valve, in the discreteness of the brachial supports, which form a double track on the dorsal surface when the shell is eroded or seen in section.

DISCUSSION.—The ventral morphology of *Gypidula* presents no departures from that in *Clorinda*, *Pentamerella*, and other genera of this subfamily. The septum is exceedingly variable in its length and this is true likewise of the spondylium. The latter in some species (*G. romingeri* and *G. coeymanensis*) is free for more than three-fourths its length. The internal surface is marked with elongate pustules and low ridges which are interpreted usually as evidences of ovarian structures. The teeth are sharp and slender.

The dorsal interiors of *G. coeymanensis* and *G. romingeri*, of which excellent examples are at hand, are especially instructive in illustrating the characters of the genus. In these the dorsal septal plates are divisible clearly into three parts, termed by Leidhold¹³ (1) inner crural plates, (2) outer crural plates, and (3) septal plates (see pp. 164-165).

A linear cardinal process was observed by Hall and Clarke in the genotype, but the occurrence of such a structure is not general throughout the various members of the genus. The usual condition is for the diductors to attach to the floor of a deep pit under the beak. It has been noted in some instances that the pit is divided by a low ridge which may be interpreted as a cardinal process, although it was apparently never functional as such in the sense of bearing the muscles.

Hall founded the genus *Gypidula* on *Pentamerus occidentalis* and *G. laeviusculus* and stated distinctly that the lamellæ of the dorsal valve were separate and diverging. This therefore excludes from *Gypidula* shells like *Sieberella sieberi* in which the septal lamellæ unite with a median septum. Hall and Clarke, reasoning with no knowledge of homœomorphy and the confusion it may cause by obscuring the true relationships of genera, maintained that the union or divergence of the crural lamellæ was of little import, being only of specific value. In so holding, they could find no distinction between the two genera except that *Sieberella* was lacking in "deltidial plates" and a "cardinal area." This distinction between the genera has been perpetuated by most recent authors. Schuchert in 1897 placed *Sieberella* in the synonymy of *Gypidula*

¹³ Abh. preuss. geol. Landesanst., N. F., Heft 109, 1928, pp. 49-53.

and this was also Leidhold's solution (1928).¹⁴ In 1913,¹⁵ however, the former author indicated *Sieberella* as a subgenus of *Gypidula* and in the Zittel-Eastman Text-book of Paleontology both were given independent rank. Recently Belanski (1928), in a study of the Iowa Upper Devonian pentamerids, notes the internal differences mentioned by Hall and Clarke and also the fact that *Sieberella sieberi* actually has a cardinal area. The latter fact has been corroborated by the present writers. This heretofore superficial distinction therefore fails, with the result that the chief difference between the genera lies in the dorsal interior. It is just as correct to assume a line of reasoning diametrically opposed to that of Hall and Clarke:

commissure sulcate; ventral fold usually defined only on the front half of the shell. Ventral interarea rather wide for the subfamily, curved, apsacline, delthyrium open, beak incurved strongly, umbo inflated. Dorsal interarea obsolete, beak incurved, umbo swollen. Surface multicostate; shell substance fibrous, impunctate.

Ventral interior.—Like *Gypidula*.

Dorsal interior.—The tripartite character of the cardinalia is essentially the same as that of *Gypidula*, but the septal plates, instead of uniting directly with the floor of the valve, unite with a low median septum.

GEOLOGIC RANGE.—Silurian and Devonian of North America and Europe.

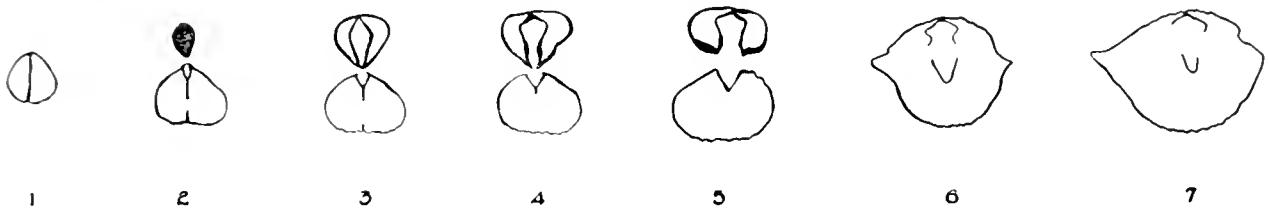


FIG. 31.—*Sieberella sieberi* Barr. Sections showing internal structure. Of greatest significance is the union of the dorsal septa to form a single plate. Distance of sections from beak:

| | |
|-----------|-----------|
| 1—1.6 mm. | 5—4.8 mm. |
| 2—2.8 | 6—7.9 |
| 3—3.5 | 7—9.2 |
| 4—4.0 | |

the internal structures can be seized upon as diagnostic, the cruralium of *Sieberella* distinguishing that genus from *Gypidula*, which has divergent lamellæ. The striking external resemblance in form we therefore attribute to homœomorphy.

Genus SIEBERELLA Oehlert 1887

Pl. 26, figs. 25, 30, 33; t. fig. 31

Oehlert in Fischer, Man. Conch., 1887, p. 1311.
Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, pp. 241, 246, pl. 72, figs. 4, 5, t. fig. 176.

GENOHOLOTYPE.—*Pentamerus sieberi* Von Buch in Barrande 1847, Brach. Sil. Schichten Boehmen, p. 103, pl. 21, figs. 1, 2.

DESCRIPTION. *Exterior*.—Outline galeatiform as in *Gypidula*, hinge-line faintly arcuate; cardinal extremities rounded. Lateral profile biconvex, the ventral valve usually with the greater convexity. Anterior

AMERICAN SPECIES

Sieberella emarginata Belanski 1928
S. insolita Belanski 1928
S. roemeri Hall and Clarke 1893 (in part)

EUROPEAN SPECIES

Sieberella multistriata Roemer
S. sieberi (V. Buch) 1847
S. sieberi rectifrons (Barrande) 1879

DISCUSSION.—Hall and Clarke restricted the name *Sieberella* to shells not having a cardinal area on the ventral valve, this being their sole distinction. A re-study of the genotype, however, shows that it possesses a well defined area. Nevertheless, there is a fundamental internal difference, the convergence of the septal plates to meet a median septum. This type of structure is not common and is restricted seemingly to rather transverse shells which are costate over nearly the whole surface. *Sieberella* has the fold restricted to the ventral valve and is thus a homœomorph of *Gypidula*. The two genera form a striking example of internal variation combined with a stable external expression.

¹⁴ Op. cit., p. 50.

¹⁵ Maryland Geol. Surv., Lower Devonian, p. 342.

Genus *PENTAMERELLA* Hall 1867

Pl. 26, figs. 4, 13-17, 19, 20; t. fig. 32

Hall, 20th Rept., N. Y. State Cab., 1867, p. 163.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, pp. 242, 245, pl. 71, figs. 21-29.

GENOLECTOTYPE (Hall and Clarke).—*Atrypa arata* Conrad 1841, 5th Rept. N. Y. Geol. Surv., p. 55.

DESCRIPTION. *Exterior*.—Outline subtriangular to subpentagonal; hinge-line narrow; cardinal extremities rounded; lateral profile biconvex, the ventral valve having the greater convexity. Anterior commissure uniplicate; dorsal fold usually low, in some species nearly obsolete. Ventral interarea narrow, curved, apsacline, beak incurved strongly, umbo swollen; del-

P. intralineata (Winchell) 1866*P. missouriensis* Branson 1922*P. pavilionensis* (Hall) 1860

DISTINGUISHING CHARACTERS.—Externally *Pentamerella* most closely resembles *Gypidula*, but differs in having the fold on the dorsal valve. Internally, it is similar to *Sieberella* in having the septal plates unite with a low septum to form a cruralium.

DISCUSSION.—Of interest in *Pentamerella* is the extremely short septum of some of the species. In shells referred to *P. pavilionensis*, from Moreland, Kentucky, the septum may be confined to the very posterior of the shell as a short rib. In the brevity of its septum *Pentamerella* represents an advanced generic development.

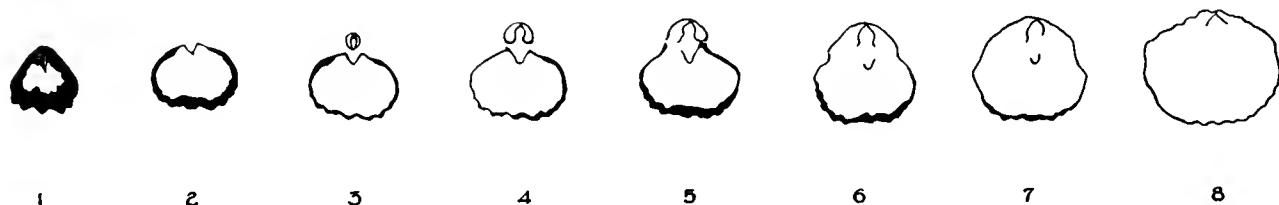


FIG. 32.—*Pentamerella* aff. *P. pavilionensis* (Hall), Alpena, Michigan. Of prime interest in these serial sections is the extreme brevity of the median septum in the ventral valve. It was apparently a ridge on the posterior wall of the shell. x 1. Distance from beak:

1—1.9 mm.

2—3.9

3—4.2

4—4.9

5— 5.5 mm.

6— 6.9

7— 7.6

8—11.25

thyrium with *incipient deltidial plates*. Dorsal interarea obsolete, beak curved under that of the ventral valve. Surface usually multicostate, occasionally smooth. Shell substance fibrous, impunctate.

Ventral interior.—Teeth narrow and sharp; spondylium duplex shallow; floor of spondylium longitudinally striated, supporting septum short; internal umbo-lateral ovarian spaces pustulose.

Dorsal interior.—Notothyrial cavity deep; plates supporting brachial processes broad and flat, supported by thin curved plates which unite in the mid-line of the shell to form a cruralium that in some specimens is supported by a low duplex septum. In the apex is a shallow pit divided by a low ridge; the two pits are the areas of the diductor scars.

GEOLOGIC RANGE.—Devonian (Middle and Upper) of North America.

SPECIES

Pentamerella arata (Conrad) 1841*P. dubia* (Hall) 1860*P. fultonensis* Branson 1922

Booker¹⁶ has recently published figures of "*Pentamerella*" *molongensis* Mitchell, which are obviously not of this genus. In this form the septal plates are widely divergent as in *Clorinda* or *Gypidula*. The same is true also of "*Pentamerella*" *sublinguifer* Maurer, figured by Leidhold.¹⁷ In this shell the dorsal septa are wide-spread and the form is certainly not a *Pentamerella*. The figures suggest *Clorinda*, as the shell is quite smooth.

Hall and Clarke say that in *Pentamerella* "there are occasionally evidences of lateral, erect or convex growths upon the margins of the delthyrium, which may be interpreted either as remnants of a resorbed convex deltidium, or as highly accelerated secondary deltaria" (pp. 341, 342). We have also seen these plates, and interpret them as incipient deltidial plates.

¹⁶ Jour. Proc. Roy. Soc. N. S. Wales, vol. 60, 1926, pp. 140-142.

¹⁷ Abh. preuss. geol. Landesanst., N. F., Heft 109, 1928, p. 57, pl. 4, fig. 14, t. fig. 25.

Genus **ZDIMIR** Barrande 1881

Barrande, Syst. Sil. Centre Bohême, vol. 6, 1881, p. 171, pl. 292, figs. 17-20.

GENOHOLOTYPE.—*Z. solus* Barrande.

DISCUSSION.—A single isolated valve from the Devonian of Bohemia, of "unusual and enigmatic" appearance, was named *Zdimir* and provisionally referred by Barrande to the Pelecypoda. The specimen, according to the author, resembles the arched valve of certain elongate pentamerids, but is slightly inequilateral. He states further that the specimen has a moderately developed, curved beak, almost as in the pentamerids, without trace of an area, and the surface of the beak is broadly open. The exterior is ornamented by costæ diverging from the beak. No muscle or pallial marks were observed. Aside from the allusions to its possible affinities with the pentamerids, Barrande compares the specimen with *Isocardia* and places it in the Pelecypoda.

It was later referred to as scarcely separable from *Uncites gryphus* by Frech.¹⁸ Novak,¹⁹ however, studied and prepared a specimen of *Z. solus* in the Bohemian museum at Prague, showing that fragments of the shell substance adhering to it had the structure of brachiopod shells and that it had a spondylium supported by a septum. *Zdimir* is therefore quite clearly a pentamerid. In 1913 Schuchert²⁰ considered the genus as a synonym of *Conchidium*. The latter genus is, however, not certainly known in the Devonian.

Barrande has described many species of *Gypidula* from Bohemia but Novak claims that *Zdimir* is not referable to any of them. Two courses can be taken with this doubtfully valid genus: (1) the name can be restricted to the existing specimens; or (2) it can be placed provisionally as a synonym of *Conchidium* which is known doubtfully from the Devonian.

Subfamily **PENTAMERINÆ** Waagen 1883

Large, rostrate, elongate, non-galeate Pentameridæ, usually without distinct interareas. It is in this subfamily that the internal characters of the family are typically developed. Shells smooth, costate or multicostate.

GEOLOGIC RANGE.—Silurian and early Devonian.

Has the following genera:

Læves

Pentamerus Sowerby

Pentameroides Schuchert and Cooper

Lissocælina Schuchert and Cooper

Capelliniella Strand

Holorhynchus Kiaer

Harpidium Kirk

Costatæ

Rhipidium Schuchert and Cooper

Conchidium Linnæus

Brooksina Kirk

Platymarella Foerste

Cymbidium Kirk

Virgiana Twenhofel

The genetic relationships are thought to be as shown in Table 20.

DISCUSSION.—The Pentamerinæ are a large and interesting group of shells intimately tied together by their rather elongate and non-galeate form as compared with the Gypidulinæ. Internally their spondylium is like that of the other subfamily. In the dorsal interior the only difference of note lies in the septa, which are less bowed than in the Gypidulinæ.

The subfamily is provisionally divided into two groups on the basis of its external sculpture. The significance of this division is discussed in the preliminary remarks. Suffice it to say here, that nearly every smooth stock is represented by an equivalent costate one. For example, *Pentamerus* represents a flattish smooth stage, and has its costate equivalent in *Rhipidium*.

The writers found that *Orthotropia*, which has long been classified with the Pentamerinæ, is actually an orthid. In the ventral valve it has a pseudospondylium and in the dorsal there is a short cruralium occupied by a prominent, simple cardinal process. The structure of *Orthotropia* allies the genus with *Linopectora*, but its exterior is at present unknown.

Læves or Smooth Pentamerinæ

Genus **PENTAMERUS** Sowerby 1812

Pl. 27, figs. 4, 8, 9, 10, 12, 15, 17-19; pl. 29, fig. 11; t. fig. 26

Sowerby, J., Min. Conch., vol. 1, 1812, p. 73, pl. 28.

Davidson, Brit. Foss. Brach., vol. 1, Introd., 1851-1855, p. 97; vol. 3, pt. 7, 1866-1871, pl. 18, figs. 1-12, pl. 19, figs. 1, 2 (*oblongus*).

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1895, p. 236, pl. 67, figs. 11-13, 20, pl. 68, figs. 1-8, pl. 69, figs. 1-14, pl. 70, figs. 1-5, t. figs. 169-171 (all of *oblongus*).

Syn. *Pentastère* Blainville 1824, Dict. Nat. Sci., vol. 32, p. 301.

GENOLECTOTYPE (Hall and Clarke).—*P. lævis* Sowerby 1812.

DESCRIPTION. *Exterior*.—Shell large, pentagonal-hexagonal in outline, commonly trilobate in front;

¹⁸ Zeits. deut. geol. Gesell., vol. 38, 1886, p. 920.

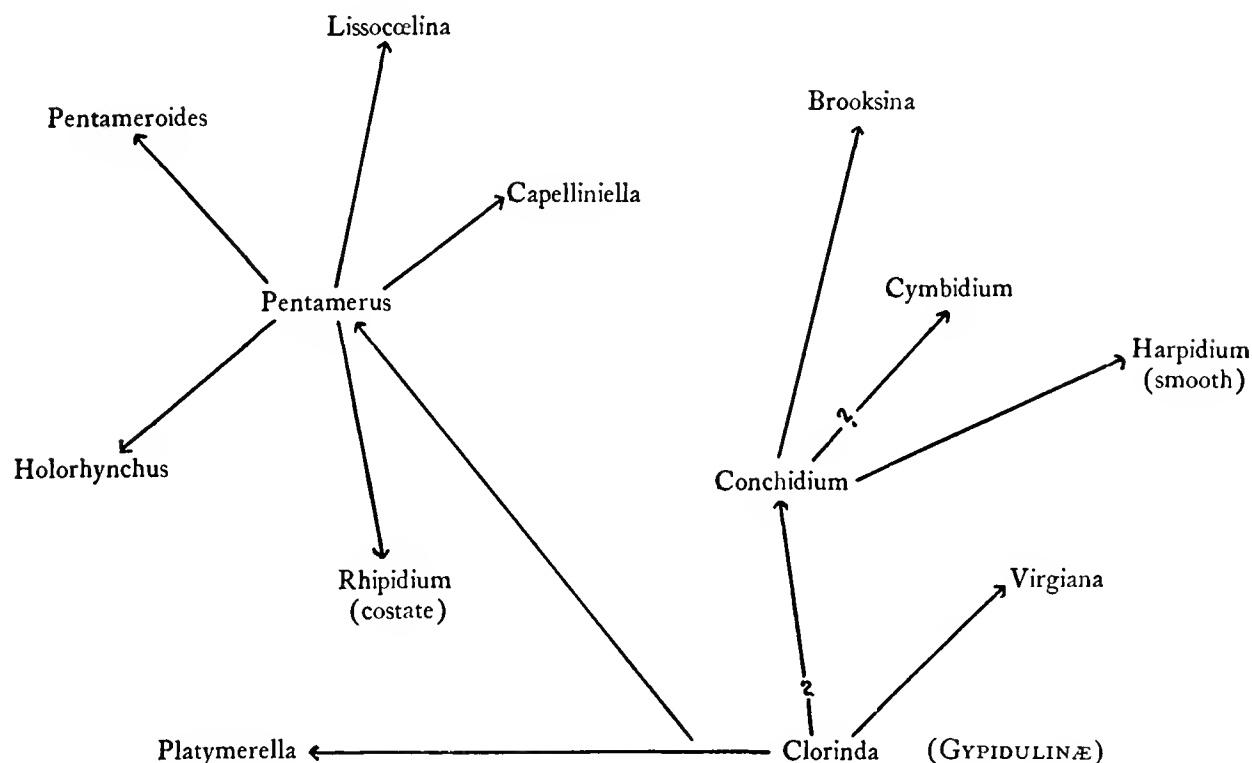
¹⁹ Ibid., vol. 40, pp. 588-590, 1888.

²⁰ Zittel-Eastman Text-book of Paleontology, 2d ed., vol. 1, p. 394.

hinge-line gently arcuate; cardinal extremities rounded; lateral profile subequally biconvex. Anterior commissure usually rectimarginate. Fold present or absent on both valves. Interareas obsolete; ventral beak curved over the dorsal; umbo prominent. Surface

P. cylindricus Hall and Whitfield 1872
P. divergens Foerste 1909
P. oblongus Sowerby 1812
P. ovalis Hall 1852
P. parvulus Savage 1913
P. pesovis Whitfield 1882

Table 20



smooth or with faint undulations at the front. Shell substance fibrous, impunctate.

Ventral interior.—The dental plates are convergent and with their septal plates unite to form a spondylium duplex.

Dorsal interior.—A tripartite division of the crural plates is recognizable. Thin inner plates unite with the walls of the valve to form lateral chambers. The sockets are notches in the partitions of these chambers next to the wall of the valve. The brachial processes are long. The septal plates are discrete, divergent or parallel, continued to the internal surface of the valve. Between the septal plates a low median septum divides the septal chamber into two parts. The cardinal process is a callosity under the beak.

GEOLOGIC RANGE.—Throughout the Silurian of Europe and North America and probably widely elsewhere.

AMERICAN SPECIES

Pentamerus bisinuatus McChesney 1861
P. compressus Kindle and Breger 1904
P. corrugatus Weller and Davidson 1896

EUROPEAN SPECIES

Pentamerus borealis Eichwald 1842
P. esthonus Eichwald 1860?
P. gothlandicus Lebedeff 1892
P. laevis Sowerby 1812
P. oblongus Sowerby 1812
P. samojedicus Keyserling 1846
P. schmidtii Lebedeff 1892

DISTINGUISHING CHARACTERS.—The genus *Pentamerus* is characterized by its comparatively smooth exterior, long spondylium duplex, discrete septal plates, and tripartite cardinalia.

DISCUSSION.—Hall and Clarke state that *Pentamerus* "is an exceedingly plastic type," and limit the name to smooth shells typified by *P. laevis* Sowerby. The latter is considered by European paleontologists as the young of *P. oblongus*.

The specific name *P. oblongus* has in America been applied to a wide variety of forms, among them *P. oblongus subrectus* Hall and Clarke. In this form the septal plates of the cardinalia are united to form a duplex septum which supports a shallow cruralium.

This development is so different from *Pentamerus* that we are distinguishing it as a new genus under the name *Pentameroides*.

The most interesting internal feature of *Pentamerus* is the long brachial process which reaches to the anterior end of the spondylium. The two processes appear to remain separate, judging by serial sections prepared by us.

Genus PENTAMEROIDES Schuchert and Cooper 1931

Pl. 27, figs. 13, 14; pl. 28, figs. 19, 22; t. fig. 27
Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 248.

GENOHOLOTYPE.—*Pentamerus subrectus* Hall and Clarke, 1893, Pal. N. Y., vol. 8, pt. 2, p. 238, pl. 69, figs. 2, 3, 8-10.

DISTINGUISHING CHARACTERS.—Externally the members of this genus are precisely like *Pentamerus*, but internally there is a cruralium in the dorsal valve that in some specimens is sessile for a short distance at the posterior but is elevated at the front. In some species, however, the cruralium is supported by a prominent median septum for its whole length. In all of the species the dorsal septum is rather long and is not uncommonly longer than the ventral one. A careful study of internal molds, a common mode of occurrence of the genus, shows that the adductor muscles were attached to the upper surface of the cruralium, for no trace of muscle scars has been observed on the floor of the valves.

We have selected *Pentamerus subrectus* as the type of the genus. This is a well defined species characterized by its shouldered dorso-lateral extremities. There are a number of unnamed species occurring in the Wisconsin dolomites, especially at Bailey's Harbor. Here occurs a flat form much like the Clinton *P. oblongus*, but another type externally nearly identical with *Pentamerus cylindricus* is also known.

DISCUSSION.—*Pentameroides* has a wide distribution in Silurian strata, being fairly common in Iowa and Wisconsin. It was also found associated with a small *Stricklandia* in the Silurian beds on the shore of the Bay of Chaleur at Black Point postoffice, New Brunswick. Some of the shells called *Pentamerus borealis* by European writers are of this type. It is thus clear that there must be a drastic revision of the species of *Pentamerus sensu lato*.

GEOLOGIC RANGE.—Widely distributed in the Silurian of North America and Europe, but the species are not at all worked out, being referred to other genera and mainly to *Pentamerus*.

AMERICAN SPECIES

P. subrectus Hall and Clarke 1893

Genus LISSOCÆLINA Schuchert and Cooper 1931

(Gr. *lissos*, smooth; *koilia*, belly)

Pl. 28, figs. 7, 14, ? 13, ? 15, ? 16, ? 21

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 248.

GENOHOLOTYPE.—*Pentamerus pergibbosus* Hall and Whitfield 1875, Pal. Ohio, vol. 2, p. 139, pl. 7, figs. 10, 11.

DISTINGUISHING CHARACTERS.—This name is proposed for smooth shells having the external form of *Conchidium* in profile and outline and the internal structure of *Pentamerus*. It represents an offshoot from the *Pentamerus* line in the Middle Silurian. The genotype is perhaps the best known example. The ventral valve is elongated and the ventral beak is arched over that of the dorsal valve as in *Conchidium*. In *Pentamerus sensu stricto* there is not the great development of the beak and the strong arching of the valves. Even in the young of "*pergibbosus*" the same shape of the adult is faithfully preserved and forbids any relationship with *Pentamerus s. s.* In the ventral interior the median septum is extremely long and in the dorsal valve the septa are rather close together and subparallel as in *Pentamerus*. Externally the shell preserves no trace of radii.

We are placing in this association, but somewhat doubtfully, *P. maquoketa* Hall and Clarke. In this species the ventral septum is short and in this respect suggests *Harpidium* but otherwise agrees fairly well with that of *Lissocælina*.

Subgenus CAPELLINIELLA Strand 1928

Strand, Arch. Naturgeschicht., Berlin, vol. 92, A8, 1928, p. 38.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, p. 248, pl. 70, figs. 6-14.

Hom. *Capellinia* Hall and Clarke 1893.

GENOHOLOTYPE.—*C. mira* (Hall and Clarke) 1893.

DESCRIPTION. *Exterior.*—Subpentagonal in outline; hinge-line exceedingly narrow; cardinal extremities obsolete. Anterior commissure rectimarginate. Lateral profile unequally biconvex, the dorsal valve always with the greater convexity. Ventral interarea exceedingly narrow, almost obsolete. Delthyrium open. Dorsal interarea obsolete, beak strongly curved, umbo swollen. Surface marked by obscure radiating costæ and a broad low fold on each valve as in *Pentamerus*. Shell substance fibrous, impunctate.

Interior.—Essentially as in *Pentamerus*.

GEOLOGIC RANGE.—Silurian of Wisconsin.

DISCUSSION.—Specimens of this subgenus appear to be rather rare and restricted geographically to Wis-

consin. It forms a remarkable example of reversion of relative convexity of the valves and from its comparatively smooth shell is clearly an offshoot from *Pentamerus*. The ventral median septum is rather long, reaching about to the middle of the valve. It extends practically to the beak, showing the spondylium to have been supported for its whole length. The spondylium as shown on interiors is, however, rather short, shorter than usual in *Pentamerus*. In the dorsal valve the septal plates are rather closely placed and nearly parallel. The portion bounded by them is divided by a low median ridge as is usual in the pentamerids.

Genus *HOLORHYNCHUS* Kiaer 1902

Pl. 27, fig. 20

Kiaer, Norg. geol. unders. aarbog for 1902, 1902, p. 68, figs. 1-7, pp. 103-110.

GENOHOLOTYPE.—*H. giganteus* Kiaer 1902.

This name was proposed by Kiaer for shells externally like *Pentamerus oblongus* Sowerby except that they are transverse and have a free spondylium in the ventral valve. The structure of the dorsal valve is like that of *Pentamerus*.

GEOLOGIC RANGE.—The only known form, the genotype, is from the Silurian of Norway.

Genus *HARPIDIUM* Kirk 1925

Kirk, Proc. U. S. Nat. Mus., vol. 66, 1925, pp. 1-5, pl. 1, figs. 1-6, pl. 2, fig. 7.

GENOHOLOTYPE.—*H. insignis* Kirk 1925.

DESCRIPTION. *Exterior*.—Shells large, longitudinally subtriangular; hinge-line narrow; cardinal extremities obsolete. Lateral profile unequally biconvex, the ventral valve usually having the greater convexity. Anterior commissure emarginate, sulci of both valves rather shallow. Interareas obsolete or exceedingly narrow. Beaks of both valves strongly arched, the ventral one bent over that of the dorsal. Beaks acutely pointed; umbo swollen; delthyrium covered by a prominent deltidium. Shell thick, fibrous, impunctate.

Ventral interior.—Spondylium duplex long and narrow, septum short.

Dorsal interior.—As in *Conchidium* and *Pentamerus*, there are three sets of plates. The inner ones form chambers at the back of the valve; the outer ones bear long brachial processes and are supported by low septa. The septal plates are subparallel and always discrete.

SPECIES

Harpidium insignis Kirk 1925
H. latus Kirk 1925
H. rotundus Kirk 1925

DISTINGUISHING CHARACTERS.—*Harpidium* may be recognized easily by its smooth exterior, strongly incurved beaks, unusually long spondylium and very abbreviated septum.

DISCUSSION.—This very interesting genus has obvious similarities to *Conchidium*. These are seen in the elongate beaks, the disproportionate size of the valves, and the whole physiognomy of the shell. Further, *Harpidium* and *Conchidium* have the peculiar concave type of deltidium, the only instances of its occurrence in the Pentameridæ.

Despite these obvious relationships there are two points of difference of considerable significance. One of these is the smooth surface which, together with the external configuration, makes this shell unique. The other difference is found in the abbreviated septum. In typical *Conchidium* the septum extends for nearly the full length of the valve and supports the spondylium for nearly its entire length. In *Harpidium*, on the other hand, the septum is unusually short and the spondylium hangs free for nearly its whole length. In one specimen the length of the septum is 17 mm., that of the spondylium about 54 mm., with a greatest width of 1.5 mm., while the length of the shell measures 75 mm. One wonders how the spondylium, hanging free as it does, can be strong enough to serve as the seat of attachment of the opening and closing muscles of the shell. Strength is evidently obtained by the narrowness of the spondylium and the broad surface of muscle attachment.

Of most interest in *Harpidium* is the deltidium, which Kirk described as "convex, elevated, deltidial plates." These are, however, not deltidial plates, but are the protruding sides of the deltidium, which is a continuous plate convex postero-dorsally. This structure is like that of *Conchidium* (see pl. 29, fig. 4; t. fig. 25).

Harpidium is evidently restricted to the Silurian of the Pacific province in Alaska. At Louisville, Kentucky, occurs a species, usually called *Pentamerus per-gibbosus* Hall and Whitfield, which is externally like *Harpidium* in being smooth, but is like *Conchidium* internally, and for this shell, which represents a stage of pentameroid evolution, we have proposed the new name *Lissocœlina*.

Costatæ or Costate Pentamerinae

Genus *RHIPIDIUM* Schuchert and Cooper 1931

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 249.

GENOHOLOTYPE.—*Pentamerus knappi* Hall and Whitfield 1872, 24th Rept. N. Y. State Cab. Nat. Hist., p. 184.

This name is proposed for rather flattish shells that have commonly but erroneously been classed with

Conchidium. They are the costate equivalent of *Pentamerus* and agree in many other external details with that genus. For example, they are distinctly trilobate, the trilobation being produced by an elongate tongue extending forward from both valves. This trilobation is carried to its extreme in this genus in the species *R. trilobata* (Kindle and Breger).

Rhipidium is a contemporary of *Pentamerus*, and probably lived before *Conchidium* arrived in American seas.

Internally the genus is like *Pentamerus* in the arrangement of its septa. Externally the ribs are as a rule implanted or split at the front. Other species besides the genotype assigned to this genus are:

Conchidium multicostatum (Hall) 1860

C. nysius (Hall and Whitfield) 1872 (see Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, p. 235)

C. tenuicosta (Hall and Whitfield) 1872

C. trilobata Kindle and Breger 1904

Genus CONCHIDIUM Linnæus (1753) 1760

Pl. 28, figs. 1-6, 8-12, 17, 18, 20, 23, 26; pl. 29, fig. 4; t. figs. 25, 28, 33

Linnæus, Syst. Nat., ed. 12, vol. 2, 1760, p. 163.

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, p. 231, pl. 66, figs. 11-14.

Syn. *Gypidia* Dalman 1828, K. Vet. Akad. Handl. for 1827, pp. 93, 100, pl. 4, figs. 1a-g.

Syn. *Antirhynchonella* Quenstedt 1868-1870, Petref. Deutsch., vol. 2, pp. 231, 727.

GENOTYPE.—*C. biloculare* Linnæus 1753, Mus. Tess., pl. 5, fig. 8.

DESCRIPTION. *Exterior.*—Subtriangular to subtrapezoidal in outline, hinge-line very narrow; lateral profile biconvex, the ventral valve usually having the greater convexity. Anterior commissure rectimarginate, sulcate or uniplicate, fold and sulcus usually narrowly pointed and uncurved; delthyrium covered by a specialized "deltidium"; dorsal beak obtusely pointed, umbo more or less swollen. Shell thick in the posterior region, costate or multicostate; shell substance fibrous, impunctate.

Ventral interior.—Spondylium duplex elongate, supported by a duplex septum usually for more than one-half its length. Septum exceedingly long.

Dorsal interior.—Septal plates divergent, consisting of three parts: (1) The inner plates which form two chambers on each side of the interior, uniting laterally with the walls of the valve. The sockets are excavated in the antero-lateral extremities of these plates adjacent to their junction with the wall of the valve. (2) Outer plates. The structures noted above are supported by two diverging lamellæ which unite with the valve directly. The line of union is marked by a thickening. (3) Brachial supports. Two small plates,

expanded at the free ends and united to the thickening at the juncture of the outer plates and the inner plates. The brachial processes extend into the cavity of the valve, in some specimens, for a distance greater than the length of the septal plates. At their distal extremities they curve laterally. Between the septal plates is a low median septum, dividing the adductor impressions.

GEOLOGIC RANGE.—Late Silurian.

AMERICAN SPECIES

Conchidium arcticum Høltedahl (Rept. 2d Norw. Arctic Exped., "Fram," 1898-1902, No. 32, 1914, p. 5)

C. colletti (Miller) 1891

C. crassoradius (McChesney) 1861

C. cumberlandicum Prouty 1923

C. exponens Hall and Clarke 1895

C. greenii Hall and Clarke 1893

C. laqueatum (Conrad) 1855

C. lindenense Foerste 1903

C. littoni (Hall) 1859

C. nettelrothi Hall and Clarke 1893

C. obsoletum Hall and Clarke 1895

C. occidentale (Hall) 1852

C. scoparium Hall and Clarke 1895

C. unguiforme (Ulrich) 1886

? *C. georgiæ* Hall and Clarke 1895 (may be *Gypidula*)

EUROPEAN SPECIES

Conchidium biloculare Linnæus 1760

C. münsteri Kiaer 1901?

C. tenuistriatum Walmstedt

DISTINGUISHING CHARACTERS.—The features of *Conchidium* that distinguish it from the other Pentamerinæ are the strongly multicostate exterior, usually strongly biconvex valves, and extended beak, below which there is a narrow interarea, a wide delthyrium, and in some species a modified deltidium. Internally *Conchidium* is like *Pentamerus*.

DISCUSSION.—It will be profitable to discuss several morphologic features of *Conchidium*, i. e., the deltidium, the spondylium duplex, and the cardinalia. Deltidial plates have been reported in many of the pentamerids, such as *Gypidula*. These plates have also been termed pseudodeltidial plates by Booker.²¹ In *Conchidium*, many specimens show these thickenings along the margins of the delthyrium, but in addition they have a concave or, in some instances, an elevated plate covering the delthyrium. The two types—plates and "deltidium"—may be observed on the same specimen. Obviously, then, the thickenings along the delthyrial margin are not true deltidial plates. This statement will become more certain after a detailed

²¹ Journ. Proc. Roy. Soc. N. S. Wales, vol. 60, 1927, p. 134.

account is given of the occurrence and structure of the "concave deltidium" of *Conchidium*. This plate in most specimens is truly concave and bears a median groove giving it the appearance of having been formed by the symphysis of two plates. One specimen of *C. biloculare*, however, shows toward the end of the beak that the plate is elevated above the margins of the delthyrium, forming a cover with nearly rectangular sides. In another specimen of the same species the plate is elevated fully 3 mm. dorsally from the del-

specimens is more than half the length of the ventral shell and in some it extends for nearly the full length.

The cardinalia, are, as is usual in the Pentameridæ, the most interesting and significant structures of the genus. Here, as in *Gypidula*, *Pentamerella*, etc., three distinct "plates" can be determined. The inner crural plates are convex and unite with a narrow flat shelf forming the inner postero-lateral margins of the valve. The union is marked by a low ridge and groove which forms the suture line between the valve and plate.

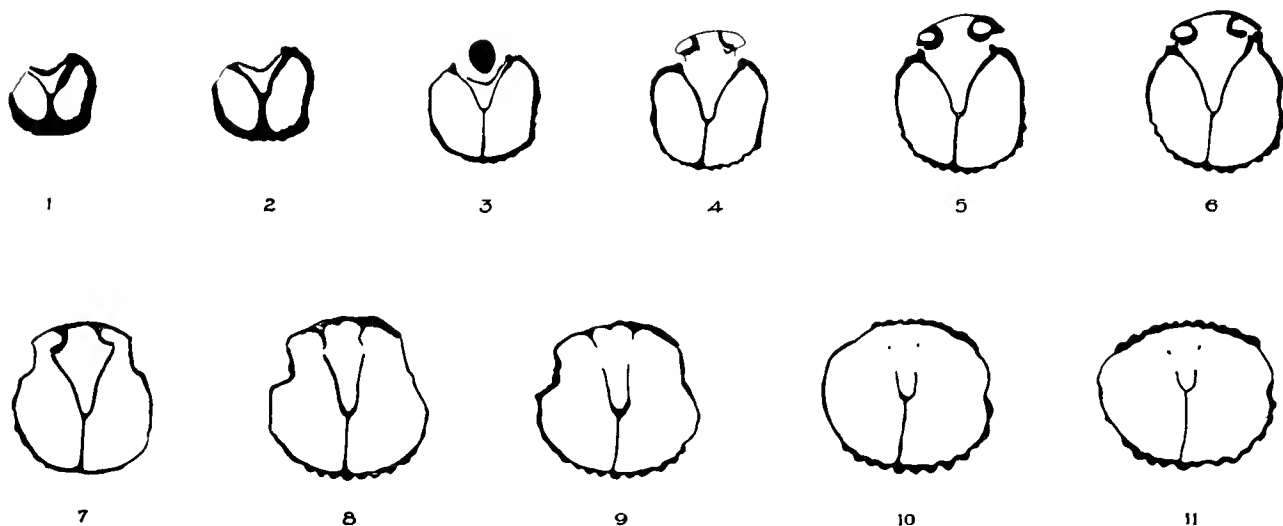


FIG. 33.—*Conchidium biloculare* Linn. Sections 1-3 show the delthyrial plate in place at a considerable distance (4.2-6.1 mm.) from the beak. It is here rather concave, having been depressed from an elevated structure like that in fig. 25. In section 4 lateral plates are visible in the dorsal valve. Similar plates were seen in *Stricklandia* (see pl. 29, fig. 6) but their function and meaning are unknown. Distance from beak:

| | |
|-----------|------------|
| 1—4.2 mm. | 7— 9.9 mm. |
| 2—5.0 | 8—11.0 |
| 3—6.1 | 9—12.1 |
| 4—7.4 | 10—14.4 |
| 5—8.1 | 11—15.0 |
| 6—8.7 | |

thyrial margin, having nearly rectangular sides, and bears a shallow median groove. There is no visible evidence that it has developed by the symphysis of two plates. Further, the "deltidial plates" are visible along the delthyrial border in specimens carrying the cover plate. This modified deltidium must therefore have been a sort of pedicle sheath housing the proximal portion of the pedicle.

Conchidium is usually defined as lacking a "cardinal area" (interarea), but in all of the specimens examined a narrow but very definite interarea could be seen.

The spondylium duplex in *Conchidium* is remarkable for the great depth of the delthyrial cavity and the great length of the septum. The latter in most

The inner plates thus form narrow lateral chambers. Posteriorly the terminations of the chambers are thickened, and together with a boss or callus beneath the beak form the "cardinal process" or seat of diductor attachment. The outer plates appear to be represented by narrow longitudinal ridges, the base of the brachial process. On the inner sides of some specimens, each of these ridges bears a plate directed dorso-medially. These are probably posterior extensions of the brachial process which extend anteriorly with a slight curve for a considerable distance; they are curved very slightly laterally but none were observed to unite into a "loop." The two inner plates and bases of the brachial processes are supported by thin divergent septal plates.

Of the species heretofore referred to *Conchidium*, several must be removed to other genera. *C. knappi*, for example, does not have the elongated and extremely incurved beak of this genus; it is essentially a rather strongly costate *Pentamerus* and belongs to our *Rhipidium*. Likewise *C. legoensis* Foerste and *C. crassiplica* Hall and Clarke do not belong in *Conchidium*, the non-bifurcation of the ribs being of little significance. Savage²² has correctly removed *C. decussatum* to the genus *Virgiana*.

Genus BROOKSINA Kirk 1922

Pl. 28, fig. 24

Kirk, Proc. U. S. Nat. Mus., vol. 60, 1922, pp. 2-5.

GENOHOLOTYPE.—*B. alaskensis* Kirk 1922.

DESCRIPTION. *Exterior*.—Transversely subelliptical in outline; hinge-line narrow; cardinal extremities obsolete. Lateral profile unequally biconvex to convexo-concave, the dorsal valve strongly convex, the ventral gently so, flat or strongly concave. Ventral interarea narrow, almost obsolete. Ventral cardinal slopes flat and defined by prominent ridges extending from the beak to the point of juncture of the costellate portion of both valves. Delthyrium probably always open. Dorsal interarea obsolete; umbo swollen. Surface of the valves multicostellate; shell substance fibrous, impunctate.

Ventral interior.—Spondylium duplex supported by a long duplex septum. Spondylium narrow but exceedingly deep.

Dorsal interior.—Septa and lamellæ as in *Conchidium* and other genera of the Pentamerinæ.

GEOLOGIC RANGE.—Upper Silurian of Alaska. Possibly Lower Devonian of the Urals.

AMERICAN SPECIES

Brooksina alaskensis Kirk 1922

ASIATIC SPECIES

Pentamerus optatus Tschernyschew 1885? (*non* Barrande)

DISTINGUISHING CHARACTERS.—*Brooksina* may be differentiated from all other pentamerids by its convexo-concave profile and costellate exterior.

DISCUSSION.—As would be expected, the interior of this genus differs somewhat from other members of the family because of the reversed convexity of its valve. The ventral septum is long and extends to the anterior margin of the spondylium. Toward the front

it is strongly corrugated. The spondylium is exceedingly narrow and deep and the anterior margin is rather straight. Postero-laterally its sides flare outward noticeably where they meet the delthyrial margins.

In the dorsal valve all parts of the cardinalia can be distinguished as in *Conchidium* and there is a long brachial process which terminates near the anterior end of the spondylium. In a specimen 30 mm. long this process is 9 mm. in length.

The young of *Brooksina* are almost equally biconvex and this gives a clue to its ancestry. It certainly must have come out of some *Conchidium* stock, perhaps out of the "*bilocularis*" line or some form resembling *C. nysius* (Hall and Whitfield). It certainly did not come out of the "*knighti*" stock, with which it is contemporaneous.

Brooksina is in the same stage of development as *Capelliniella* and is thus to *Conchidium* what *Capelliniella* is to *Pentamerus*. These two forms and *Anastrophia* are the only representatives of this stage of evolution so far observed in the pentamerids, but other "reversed" forms as aberrant developments are to be expected.

Genus CYMBIDIUM Kirk 1926

T. fig. 34

Kirk, Proc. U. S. Nat. Mus., vol. 69, art. 23, 1926, p. 2, pl. 1, figs. 5-13; t. fig. 34.

GENOHOLOTYPE.—*C. acutum* Kirk 1926.

DESCRIPTION. *Exterior*.—Subelliptical in outline; lateral profile subequally convex, the dorsal valve with the greater convexity. Interareas obsolete; delthyrium open so far as known. Each side of the delthyrium bounded by a broad flattened area. Dorsal beak strongly arched, umbo swollen. Surface multicostate, shell substance fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; bounded by a free spondylium which extends for a long distance forward.

Dorsal interior.—Septal plates widely spaced, rather short. Inner plates exceedingly short. A low short median ridge exists in the middle of the notothyrial cavity.

DISCUSSION.—*Cymbidium* is a most unusual brachiopod and its careful description by Kirk leaves little to be added. Of special interest is the free spondylium, which is a very rare structure in this class of organisms. Careful sectioning by Kirk failed to reveal any trace of a septum or any evidence that the spondylium had previously been sessile. Among the pentamerids *Hol-orhynchus* is the only other genus having a free spondylium.

In the dorsal valve the septa are clearly pentameroid although not absolutely typical. Division into three

²² Jour. Geol., vol. 26, 1918, p. 335.

sets of plates is not entirely clear. The inner plates appear to be exceedingly short, making small chambers at the rear as in *Conchidium*. In front of the inner plates the septal ones are low and bear elongate processes as is usual in pentamerids.

It is difficult to trace the lineage of *Cymbidium*. From its external form it would appear to be related to *Conchidium* ("biloculare") but the spondylium is much wider than is usual in that genus. The loss of the ventral septum appears to be rare among pentamerids, and in the orthids with spondylia is seen only in the Middle Cambrian *Protorthis* and *Loperia*.

Genus PLATYMERELLA Foerste 1909

Pl. 27, figs. 2, 3, 5, 11

Foerste, Bull. Sci. Lab. Denison Univ., vol. 14, 1909, p. 70, pl. 1, figs. 1A-D; vol. 19, 1920, p. 223, pl. 23, fig. 5.

AMERICAN SPECIES

Platymerella manniensis Foerste 1909

Conchidium crassiplica Hall and Clarke 1895

DISTINGUISHING CHARACTERS.—*Platymerella* was distinguished by its nomenclator as unique for the following reasons: (1) absence of a straight hinge margin, (2) non-galeatiform exterior, (3) ventral and dorsal beaks approximate, (4) median septum short.

DISCUSSION.—Some time after the appearance of the original description of *Platymerella*, Dr. Foerste redescribed the genus on the basis of new material showing perfectly the character of the internal structure, which had hitherto been unknown. As shown by these specimens, the genus has essentially the same structure as *Pentamerus*, but the plates in both valves are unusually short, actually making it difficult to distinguish the ventral from the dorsal, as stated by



FIG. 34.—*Cymbidium acutum* Kirk. Sections cut through the beak of a dorsal valve, showing pentameroid character of the septal plates. Distance from beak:

1—1 mm.
2—3
3—4

4—5 mm.
5—6

GENOHOLOTYPE.—*P. manniensis* Foerste 1909.

DESCRIPTION. *Exterior.*—Longitudinally suboval, hinge-line narrow; cardinal extremities rounded. Lateral profile subequally biconvex; anterior commissure rectimarginate. Fold and sulcus indistinct, or ventral sulcus shallow and dorsal fold low. Beaks subequal, incurved. Surface multicostate; shell substance fibrous, impunctate.

Ventral interior.—Spondylium duplex short, septum short. Spondylium directed antero-dorsally. Ovarian areas marked by elongated pustules.

Dorsal interior.—Cardinalia confined to the posterior, exceedingly short. Septal plates short, discrete or united by extra shell deposit to form a small chamber which is U-shaped in cross-section, making a pseudocruralium. Brachial processes as in *Pentamerus*. In front of the pseudocruralium is a long, slender, but low median ridge. The adductors are elongate impressions on each side of the median ridge.

GEOLOGIC RANGE.—Early (and ? Middle) Silurian.

Foerste. The published description of the genus leaves little to be added now that the interiors are known. However, Foerste figures and describes two types of shells in *Platymerella*. In one of these, the septal plates of the cardinalia are united at their junction with the valve by extra testaceous substance which forms a pseudocruralium, as may be seen in Foerste's figures 5E and 5F. The other type appears in figures 5G and 5H; it shows two elongate septal plates extended for a considerable distance along the inner surface of the valve, and strongly resembles *Pentamerus*. In the type which forms a pseudocruralium there is no trace of the extensions of the septal plates forward, and, on the other hand, in the type with the elongate, parallel plates there is no evidence of a median septum. There are two possible explanations: (1) we are here dealing with homœomorphs, one type representing *Platymerella* and the other being referable to *Pentamerus*; (2) we may look at the problem from another angle and maintain that both types belong to the genus *Platymerella*, the form with the pseudo-

cruralium being developed from the type with the parallel plates by deposition of adventitious shell matter between the plates. Specimens from Mannie, Tennessee, examined by us appear to conform to the first type, that with the pseudocruralium, and it is to this form that the name must be restricted unless further acquisition of material shows that *Platymere* s. s. develops from a type with parallel plates and no adventitious material. One specimen from Illinois sectioned by us is of the *Pentamerus* type, and probably the Alexandrian species from Illinois now referred to *P. manniensis* are actually not the same species and may not be of the same genus.

Foerste has suggested that *Platymere* is closely related to *Pentamerella*. The cardinalia are suggestive of this relationship but the shape of the valves, the nature of the beaks, and the structure of the spondylium are quite different. Furthermore, there is an enormous time discrepancy between the two genera which makes the relationship rather remote. *Platymere* is of great interest because it is the earliest known pentamerid (together with the *Pentamerus*-like form referred to above). Here again a plicated form introduces a large group of shells.

Genus VIRGIANA Twenhofel 1914

Pl. 27, figs. 1, 6, 7, 16; t. fig. 35

Twenhofel, Geol. Surv. Canada, Mus. Bull. 3, 1914, p. 27.

GENOHOLOTYPE.—*Pentamerus barrande* Billings 1857, Geol. Surv. Canada, Rept. Prog. for 1856, p. 296.

DESCRIPTION. *Exterior.*—Elongate-oval, hinge-line short, lateral profile biconvex, the ventral valve having the greater convexity. Anterior commissure sulcate, uniplicate, or nearly rectimarginate. Ventral valve usually with a low fold, which in young stages forms a median plica in a low sulcus; the dorsal valve in young shells usually has a noticeable fold, which may reverse at maturity into a sulcus or may remain as a low fold. Interareas obsolete, ventral beak incurved strongly, umbo swollen; dorsal beak curved under the ventral. Surface unevenly multicostate; shell substance fibrous, impunctate.

Ventral interior.—Delthyrial cavity deep; spondylium duplex long, free anteriorly; duplex septum short.

Dorsal interior.—Dorsal valve provided with two short, stout septal plates which extend nearly vertically and attach directly to the internal surface of the valve.

GEOLOGIC RANGE.—Early Silurian of North America.

SPECIES

Clorinda barrande Billings 1857
Pentamerus decussatus Whiteaves 1891
Virgiana anticostiensis Twenhofel 1928
V. major Savage 1916
V. mayvillensis Savage 1916

DISTINGUISHING CHARACTERS.—*Virgiana* is most readily identified by its strongly convex ventral valve and relatively gently convex dorsal valve, elongate spondylium, and short, discrete septal plates.

DISCUSSION.—In the ventral valve of young individuals of *V. barrande*, for 2 or 3 millimeters there is a shallow sulcus, but after this distance a low median plica develops in the depression. As growth continues, the sulcus becomes shallower and finally disappears, but the median plica enlarges and continues to the front margin as a low fold. In some varieties the median plica consists of a bundle of low costæ. The fold at the front margin is very gentle and is usually narrow.

On the dorsal valve of young individuals of *V. barrande* the young are provided with a low plica, indented medially by a shallow stria. With continued growth and bifurcation of the median plica, the fold is lost in the ornamentation of the valve. In some specimens the antero-median portion of the valve is depressed into a very shallow sulcus. It is this phenomenon of the "reversion" of the fold and sulcus that Twenhofel considered the most important generic character of his genus. However, in the specimens from Anticosti in the Peabody Museum there are many in which the dorsal fold maintains its identity throughout the length of the valve. This is especially true of the small *V. anticostiensis*. Furthermore, some specimens of *V. mayvillensis* preserve the fold from near the beak to the front margin.

More important in the diagnosis of the genus than reversion of the fold and sulcus is the internal structure of the valves. The ventral shell has an exceedingly long spondylium which is free for most of its length. In the dorsal valve the cardinalia are remarkable for their simplicity and shortness; in one individual having a length of 36.5 mm. the septal plates extend for only 5 mm. These plates are pentameroid, uniting directly with the valve. This structure differs from that of *Clorinda* in having the plates nearly parallel in horizontal section and in not possessing the inner carinæ which project into the cavity bounded by the plates. The structure therefore is not greatly different from that of *Conchidium* and we are removing the genus to the subfamily Pentamerinæ where it properly belongs.

Hall and Clarke²³ figure an interior of *Pentamerus barrande* showing a spondylium in both valves, that

²³ Pal. N. Y., vol. 8, pt. 2, 1893, p. 243, t. fig. 174.

of the dorsal one being shallow and supported by a very low median septum. This figure is utterly incorrect and gives an entirely wrong impression of the interior of *Virgiana*. The dorsal structure of this genus is precisely like that of *Pentamerus* in composition and most nearly resembles that of *Platymarella* in the brevity of its septa.

discrete, with more or less long brachial supports. The only genus is *Stricklandia* Billings of the Silurian.

The origin of this family is not yet known, but it may have come out of camerellids. Instead of retaining the shell form of the camerellids, however, the Stricklandiæ developed into wide-hinged types. It is possible also that the stricklandids came out of a much

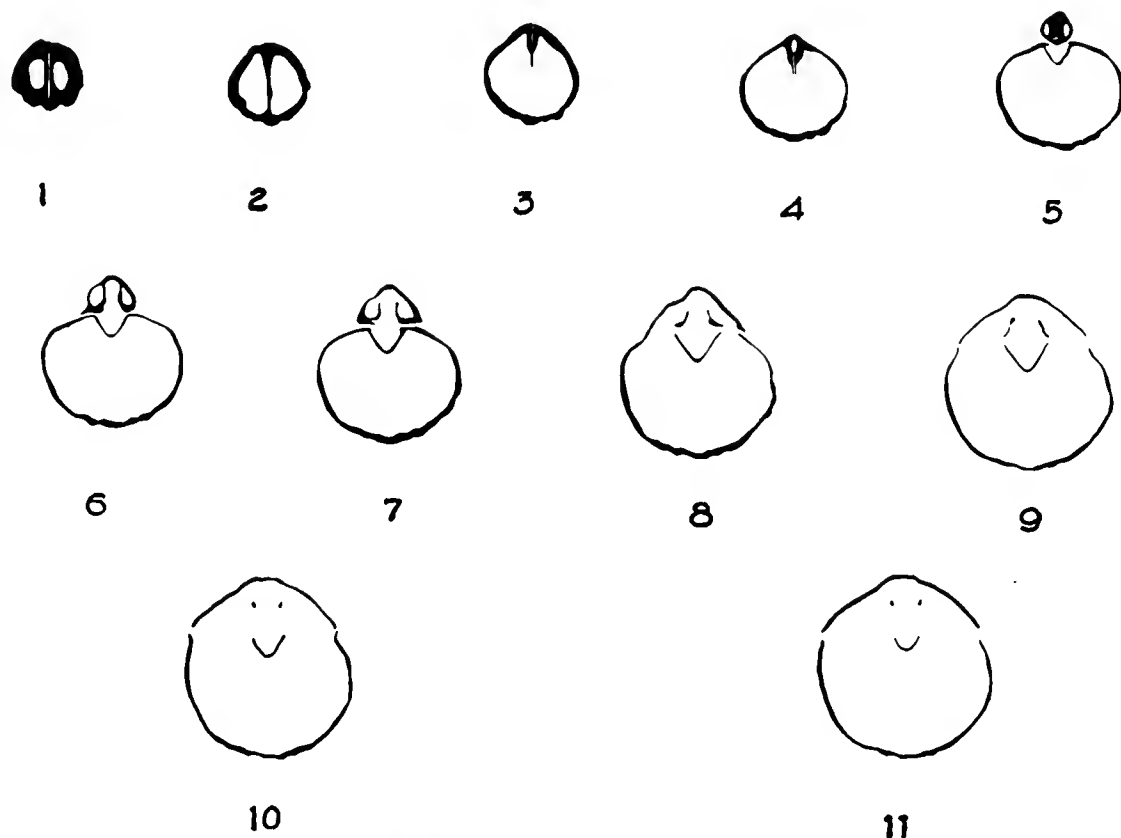


FIG. 35.—Serial sections of *Virgiana barrandei* (Billings), from Anticosti. Notice the general similarity of the structure to that of *Pentamerus s. s.*, pl. 29, fig. 11. The difference between the two genera internally is the brevity of the dorsal septa in *Virgiana*, in this specimen a little more than 2 mm. Distance from beak:

| | |
|-----------|------------|
| 1—1.0 mm. | 7— 6.4 mm. |
| 2—2.2 | 8— 7.7 |
| 3—2.9 | 9— 8.9 |
| 4—4.4 | 10—10.5 |
| 5—5.2 | 11—11.5 |
| 6—5.9 | |

The shell sectioned was 41.8 mm. in length. All trace of the spondylium disappeared at 24 mm. from the beak; the ventral septum disappeared at about 5 mm. These facts indicate an exceedingly long spondylium and very abbreviated septum.

? Family STRICKLANDIDÆ Hall and Clarke 1894

Divergent large Pentameracea, probably developed out of the Camerellidæ. Spondylium short, supporting a short septum. Cardinalia simple but specialized and

older stock, the Syntrophidæ. In neither supposition are the annectant genera known, but it is more natural to look for them in the later Ordovician, in which event the origin would be out of the camerellids.

The Stricklandias are first met with in the early Silurian of North America in faunas of northwestern

European origin, and the ancestral stock is to be looked for in the later Ordovician of Europe.

Interareas are characteristic of the Orthacea and Strophomenacea of the Protremata, and in the Telotremata are of common occurrence only among the Spiriferacea. They manifest themselves in some of the Pentameracea only and their appearance here, say Hall and Clarke,²⁴ "may be regarded as the resumption of a primitive or original character which was normal" for the Protremata.

Regarding interareas among the rostrate pentamerids, Hall and Clarke say:²⁵

Every now and then specimens will show a clearly developed cardinal area; always in *Stricklandinia*, frequently and normally in *Gypidula*, rarely and of exceptional occurrence in *Pentamerella*. *Stricklandinia* possesses so straight and long a hinge, so sharply defined an area and so short a spondylium, that it is more natural to regard this genus as the accompaniment, rather than the close organic kin of the other pentameroids, deriving its differentials directly from those long-hinged and straight-hinged shells of the early Silurian [= Ordovician], which constitute the genus *Syntrophia*.

Genus STRICKLANDIA Billings 1859

Pl. 28, figs. 25, 27, 28; pl. 29, fig. 6

Billings, Canadian Nat. and Geol., vol. 4, 1859, p. 132, figs. 8-9 (*lens*).

Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, 1893, p. 249, pl. 73, fig. 11.

Syn. *Stricklandinia* Billings 1863.²⁶

GENOLECTOTYPE (Hall and Clarke).—*S. gaspéensis* Billings 1859.

DESCRIPTION. *Exterior*.—Shells variable in size but tending to be large, elongate-oval, transversely oval, or subcircular in outline; hinge-line straight, cardinal extremities rounded. Lateral profile biconvex, the dorsal valve usually having the greater convexity. Anterior commissure rectimarginate or gently uniplicate; ventral sulcus shallow or obsolete or raised into a low fold. Dorsal fold usually present, low. Ventral interarea wide, curved, apsacline; delthyrium open. Dorsal interarea reduced, apsacline. Surface smooth or multicostate. Shell substance fibrous, impunctate.

Ventral interior.—Teeth small, dental plates short and stout, uniting to form a small spondylium duplex. Supporting septa short.

Dorsal interior.—Internally there are two slightly divergent plates which slope toward each other but do

not unite. The inner margins of the plates are thickened and give off long processes which form the arm attachments. Adductor impressions are elongate pits on the floor of the valve, the anterior pair slightly divergent distally, the posterior pair narrower and subparallel.

GEOLOGIC RANGE.—Lower and Middle Silurian.

AMERICAN SPECIES

Stricklandia anticostiensis Billings 1863

S. billingsiana (Dawson) 1880

S. brevis Billings 1859

S. breviuscula (Savage) 1916

S. canadensis Billings 1859

S. castellana (White) 1876

S. chapmani (Hall and Clarke) 1895

S. circularis (Savage) 1916

S. davidsoni (Billings) 1868

S. deformis (Meek and Worthen) 1870

S. gaspéensis Billings 1859

S. manitouensis (M. Y. Williams) 1919

S. melissa (Billings) 1874

S. multilirata (Whitfield) 1877

S. norwoodi (Foerste) 1906

S. pyriformis (Savage) 1916

S. pyriformis elongata (Savage) 1916

S. pyriformis varicosa (Savage) 1916

S. salteri (Billings) 1868

S. striata (Twenhofel) 1928

S. triplesiana (Foerste) 1885

Clorinda beccsiensis (Twenhofel) 1928

EUROPEAN SPECIES

Atrypa lens Sowerby 1839

Spirifer liratus Sowerby 1839

Pentamerus microcamerus McCoy 1859

DISTINGUISHING CHARACTERS.—*Stricklandia* is best identified externally by its lenticular outline, wide hinge-line, and well developed interarea. The spondylium and its supporting septum are very short. The cardinalia consist of two concave plates giving off long brachial processes from their posterior inner margins.

DISCUSSION.—Billings' genus differs widely from all members of the Pentameracea in several features, both internal and external. The most striking external variation is the width of the hinge-line, which is narrow in all other known members of the superfamily. Along with the wide hinge-line goes a short but wide interarea, seen best in the genotype. All of the pentamerids retain remnants of the interarea but they are confined to the margins of the delthyrium and in some species are nearly obsolete.

The spondylium is a typical duplex one, and is remarkable for the abbreviation of both the septum and the spoon. These features in themselves are of no

²⁴ Pal. N. Y., vol. 8, pt. 2, 1894, p. 336.

²⁵ Op. cit., p. 342.

²⁶ *Stricklandia*, a plant, does not invalidate *Stricklandia* Billings 1859, as that author supposed.

great taxonomic importance, but in combination with the peculiarities of the dorsal valve form a unique ensemble. The structure of the cardinalia is comparable to that of *Orthorhynchula* among the early Rhynchonellacea, is much simpler than in the Pentameridæ, but not more so than in the Camerellidæ. In *Orthorhynchula* the crural bases are concave plates hanging free in the valve and bear long, curved crural processes.

Regarding *Stricklandia*, Hall and Clarke have this to say:

These pentameroids are principally remarkable for the unusual development of the cardinal areas of both valves in the larger and more typical species, and the straight orthoid hinge in the earlier and smaller members of the group. The combination of such features with an internal chambered structure is not of frequent occurrence among these genera. [The interareas] are sharply defined on both valves, and so persistent are they that we look for the origin of this combination, not among the various pentameroids. . . but to the small, transverse shells of the early faunas to which the term *Syntrophia* has been applied,

as *Syntrophia* ? *arachne* and *S.* ? *arethusa* of the Lower Ordovician; these species, however, are not of the genus *Syntrophia* but may belong to *Huenella*. This

origin may not be the correct one, but in that event why do we not find any Ordovician stricklandid? We are therefore inclined to look for the origin of the family in the Camerellidæ, with the idea that the small inherited interareas are redeveloped into the much larger ones of *Stricklandia*.

In the dorsal valve of *Stricklandia*, according to Hall and Clarke, "the short dental plates, at their inner angles, bear long crural processes," and are analogous with those of *Amphigenia*, but do not unite to form a hinge-plate or cruralium as in that genus. On page 355 these authors erect the family Stricklandidæ for the genera *Syntrophia* and *Stricklandia*. The present authors agree that *Stricklandia* can not be incorporated in the family Pentameridæ, and we therefore accept the family Stricklandidæ but exclude from it *Syntrophia*.²⁷

²⁷ The junior author would exclude the Stricklandidæ from the Pentameroidea entirely. The cardinalia are totally unlike anything known in that order (Syntrophiacea and Pentameracea). In his opinion the best place for *Stricklandia*, so far as present knowledge goes, is among the early Rhynchonellacea.

APPENDIX

? Superfamily RHYNCHONELLACEA Schuchert 1896

Genus RHYNCHOCAMARA Schuchert and Cooper 1931

(Gr. *rhynchos*, beak; *kamara*, chamber)

Pl. 25, figs. 1, 2, 7, 17, 18

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 248.

GENOHOLOTYPE.—*R. plicata* Schuchert and Cooper 1931.

internal structure of *Rhynchocamara* is essentially rhynchonelloid, not pentameroid, since the notothyrial or subrostral chamber has much the same shape as that seen in later rhynchonellids.

GEOLOGIC RANGE.—Ordovician (Chazy), so far as known.

AMERICAN SPECIES

Camerella bella Fenton 1928

C. varians Billings 1859

Rhynchocamara plicata Schuchert and Cooper 1931

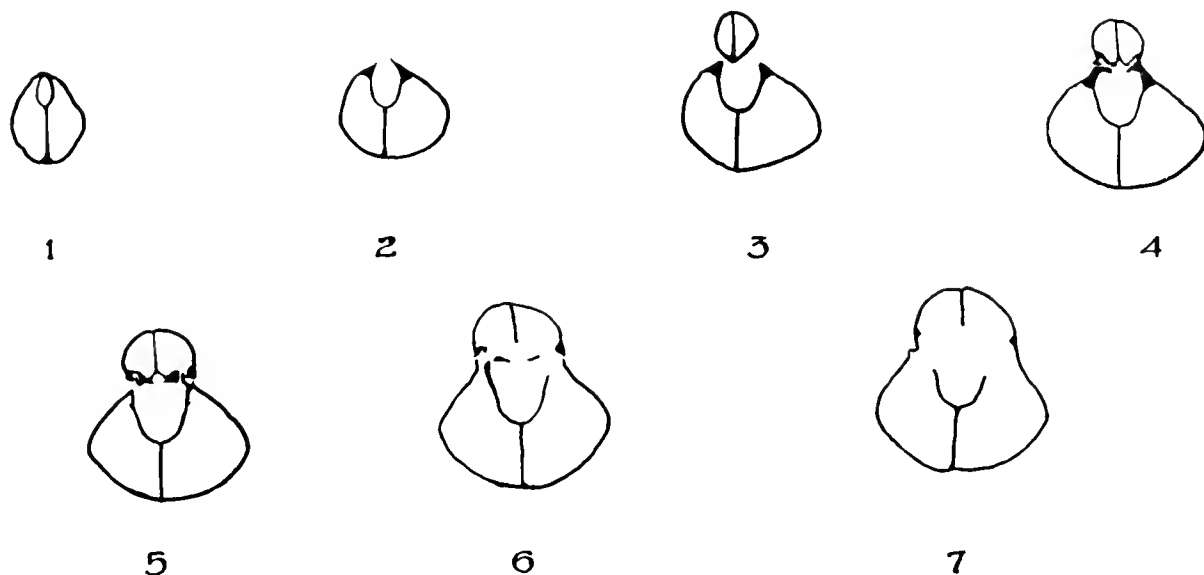


FIG. 36.—*Liocælia proxima* (Barrande). The beak and spondylium of *Liocælia* are rather strongly curved, which accounts for the peculiar oval seen in section 1. Sections 4 and 5 show the rhynchonelloid chamber in the dorsal valve.

Distance of each section from the beak:

1—1.4 mm.

2—2.6

3—3.3

4—3.5

5—4.5 mm.

6—5.2

7—6.2

In a shell 18.6 mm. in length the dorsal septum persisted for 8.5 mm. and the ventral septum was present 9 mm. anterior to the beak.

The chief distinguishing features of *Rhynchocamara* are the camerelloid exterior, short hinge-line, ventral spondylium duplex, and rhynchonelloid cruralium. From *Camerella* it differs in outline, the former being more globular, and in the structure of the dorsal valve. The cruralium duplex of *Camerella* is long and narrow, extending for perhaps one-fourth the length of the valve, whereas in *Rhynchocamara* it is confined to a small region beneath the beak. The dorsal

Genus LIOCÆLIA Schuchert and Cooper 1931

(Gr. *leios*, smooth; *koilia*, belly)

Pl. 25, figs. 31, 32, 37; pl. 29, fig. 9; t. fig. 36

Schuchert and Cooper, Amer. Jour. Sci. (5), vol. 22, 1931, p. 248.

GENOHOLOTYPE.—*Pentamerus proxima* Barrande, see Syst. Sil. Bohême, 1879, vol. 5, pl. 9, fig. 5, pl. 81, fig. 5.

DESCRIPTION. *Exterior*.—Subpentameral in outline; hinge-line narrow; lateral profile subequally biconvex; anterior commissure uniplicate, the fold and sulcus being defined at the front half. Ventral beak curved over the dorsal. Surface smooth; test fibrous, impunctate.

Ventral interior.—In the ventral valve there is a long spondylium supported for nearly its full length by a high median duplex septum which extends for nearly half the length of the valve.

Dorsal interior.—There is a small and short cruralium supported by a high septum. This cruralium is partially covered by lateral plates which overhang the notothyrial margins much as deltidial plates, representing a divided hinge-plate. In a valve about

20 mm. long the subrostral chamber is only 2 mm. in length.

GEOLOGIC RANGE.—Silurian of Bohemia.

DISCUSSION.—At first it appears difficult to assign *Liocælia* to its proper place among either the pentamerids or the rhynchonellids. The external form is essentially pentameroid, and the ventral valve with its spondylium duplex is a normal pentameroid feature. But in the dorsal valve the cardinalia are rather those of the rhynchonellids, such as *Camerophoria*, especially in the small subrostral vault. It would thus appear that *Liocælia* is essentially a smooth *Camerophoria* having an external form like that of *Clorinda*, *Merista*, or *Meristella*.

PLATES

PLATE A

Brachiopod Morphology

| | |
|--|--|
| <i>ACP</i> , accessory cardinal process | <i>FP</i> , fulcral plate |
| <i>AcS</i> , accessory dental socket | <i>Ias</i> , impression of adductor scar |
| <i>Add</i> , adductor scars | <i>LP</i> , lateral plate |
| <i>Addt</i> , adductor track | <i>Mbrp</i> , mold of brachiophore plate |
| <i>Adj</i> , adjustor scars | <i>McP</i> , mold of cardinal process |
| <i>Adt</i> , adventitious testaceous substance | <i>Mms</i> , mold of median septum |
| <i>Br</i> , brachiophore | <i>MR</i> , median ridge |
| <i>Brp</i> , brachiophore plate | <i>MS</i> , median septum and euseptum |
| <i>BrP</i> , brachiophore process | <i>Ov</i> , ovarian impression |
| <i>CF</i> , crural fossette | <i>PC</i> , pedicle callist |
| <i>Ch</i> , chilidium | <i>PFF</i> , pedicle foramen filling |
| <i>CP</i> , cardinal process | <i>PPS</i> , primary pallial sinus |
| <i>CPF</i> , crural pit filling | <i>PS</i> , pallial sinus |
| <i>D</i> , deltidium | <i>PsSp</i> , pseudospondylium |
| <i>DA</i> , duplex adductor scar | <i>SF</i> , filling of socket |
| <i>DC</i> , delthyrial cavity | <i>Sp</i> , spondylium |
| <i>DeP</i> , dental plate | <i>SPS</i> , secondary pallial sinus |
| <i>Di</i> , diductor scar | <i>T</i> , tooth |
| <i>F</i> , foramen | <i>TPS</i> , tertiary pallial sinus |

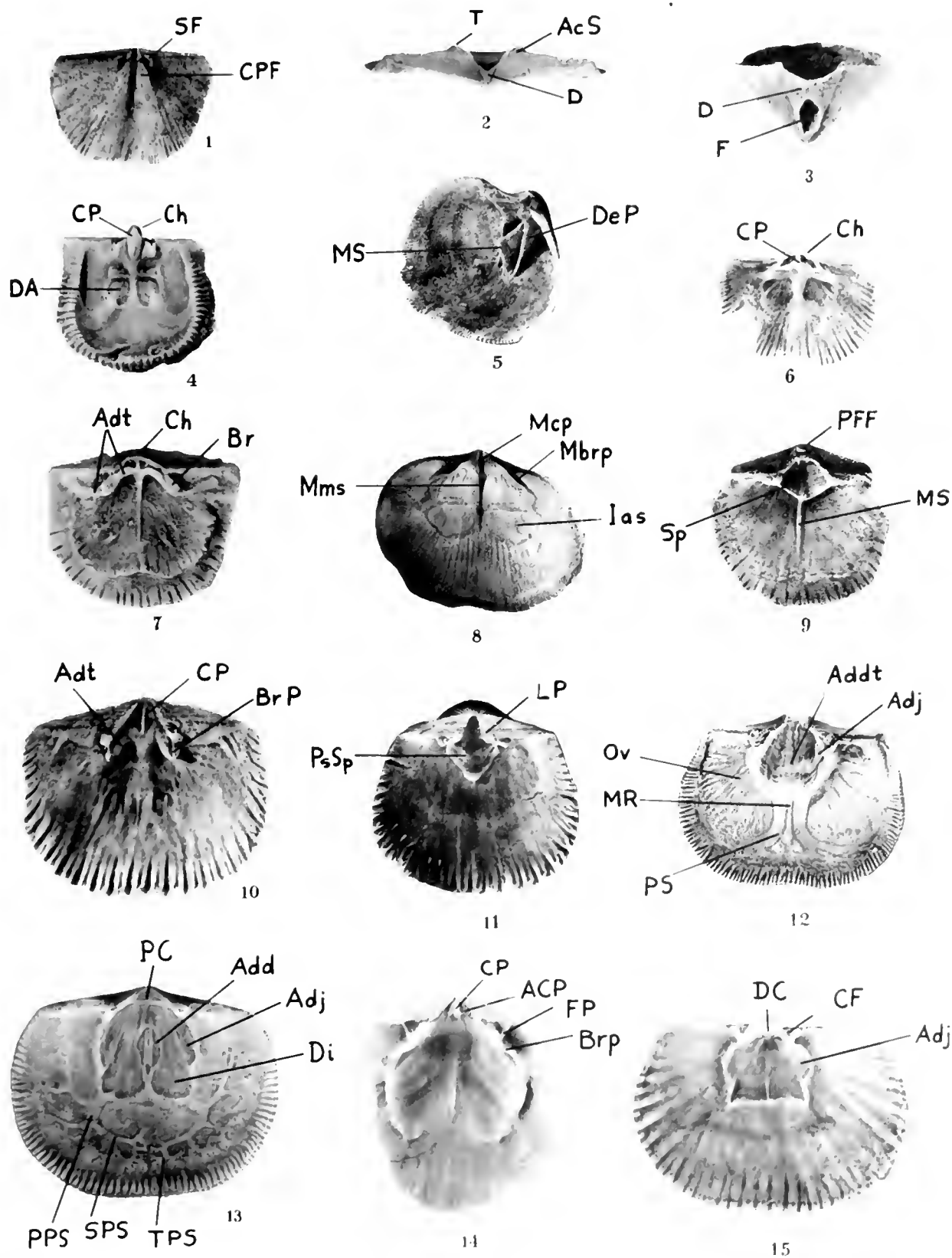


PLATE 1

FIGS. *Bohemiella romingeri* (Barrande)

- 1, 18.—Wax replicas of dorsal interior, showing cardinalia which are orthoid in aspect. Cf. pl. 4, fig. 17. Note differences from cardinalia of *Billingsella* and *Eoorthis*, figs. 13 and 28.
- 3.—Internal mold of small ventral valve, showing divergent pallial trunks.
- 22.—Wax replica of dorsal exterior. Cf. fig. 6.
Mid. Cambrian, Skrej, Bohemia. Cat. No. S12. x 2.
- 5.—Dorsal exterior, showing also ventral valve in place. Deltidium lacking and profile plano- or concavo-convex.
- 11.—Dorsal interior, showing remarkable growth of adventitious shell over brachiophores. Cf. pl. 5, figs. 17, 24. Wax impressions of molds. Mid. Cambrian, Skrej, Bohemia. Originals U. S. Nat. Mus. Cat. No. 52267. x 2.

Orusia atava (Matthew)

- 2.—Internal mold, showing slotlike molds of brachiophore plates. Erroneously referred to *Eoorthis* by Walcott. After Walcott, Camb. Brach., pl. 95, fig. 7b. x 0.5.

Orusia lenticularis (Wahlenberg)

- 7.—Ventral internal mold, showing dental plates.
- 9.—Dorsal internal mold, showing slotlike molds of brachiophore supporting plates, probably very similar to those of *Finkelnburgia*.
After Walcott, Camb. Brach., pl. 98, figs. 2d, 2f'.
Reduced.

Oligomys exporrectus (Linnarsson)

- 4, 15.—Ventral internal mold, showing impression of small delthyrial cavity and muscle tracks.
Mid. Cambrian (Paradoxides zone), Westrogothia, Lovened, Sweden. Cat. No. S 16. Fig. 4 x 2.65; fig. 15 x 6.
- 8.—Dorsal interior, showing cardinalia. Cf. *Billingsella*, fig. 13. The brachiophores of *Oligomys*, when complete, are similar to those of *Orthis s. s.* Replica of specimen figured by Walcott, Camb. Brach., pl. 88, fig. 11.
- 17.—Dorsal internal mold, showing pallial marks. After Walcott, Camb. Brach., pl. 88, fig. 1k. Reduced.
Mid. Cambrian (*Agnostus laevigatus* zone), Gudheim, 12.5 miles SSE of Skara, Sweden. Cat. No. 52249 U. S. Nat. Mus.

Billingsella cf. pepina (Hall)

- 6, 19.—Dorsal and ventral exteriors, showing ornamentation.
- 13.—Dorsal interior, showing cardinalia. Note short brachiophores. Cf. *Eoorthis*, fig. 28.
- 21, 25.—Ventral interiors, showing perforate deltidium. Fig. 25 shows thickening of median portion of muscular area. Note the large teeth. The deltidium is an arch as in other orthoids. Cf. pl. 7, fig. 16.
Up. Cambrian, Grand Teton, S. of Muskrat Lake, Teton Creek, Idaho-Wyoming state line. Cat. No. S 2220. x 2.

FIGS. *Billingsella lindstroemi* (Linnarsson)

- 10.—Ventral internal mold, showing divergent pallial trunks and reniform ovarian impressions. Cf. *Orthis*, pl. 2, fig. 18. After Walcott, Camb. Brach., pl. 87, fig. 6e. Reduced.
Mid. Cambrian (*Paradoxides forchhammeri* zone), Alunbruk, Oeland I., Sweden.
- 27.—Ventral internal mold, showing pallial markings and adherent fragments of shell. A thin section of the shell substance (see pl. 29, fig. 12) shows it to be fibrous, and fibres are visible with a hand lens also.
Mid. Cambrian (Paradoxides zone), Westrogothia, Lovened, Sweden. Cat. No. S 20. x 2.

Protorthis billingsi (Hartt)

- 12.—Ventral internal mold, showing free spondylium.
Cambrian (Acadian), Seeley St., St. John, N. B. Cat. No. S 94. x 2.65.
- 14.—Ventral valve, showing free spondylium.
After Hall and Clarke, Pal. N. Y., vol. 8, pt. 1, 1892, pl. 7A, fig. 16. Reduced.

Nisusia festinata (Billings)

- 16.—Wax replica of exterior of a small ventral valve.
Low. Cambrian, near Emigsville, York Co., Penn. Cat. No. S 9. x 2.
- 20.—Dorsal internal mold, showing musculature. Cardinalia similar to those of *Billingsella* but more primitive. After Walcott, Camb. Brach., pl. 100, fig. 1g. Reduced.
Low. Cambrian, near Emigsville, Penn.

Eoorthis remnicha (Winchell)

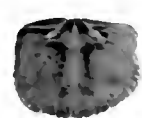
- 23.—Dorsal interior, showing cardinalia. A low cardinal process or ridge has risen between the seats of muscle attachment on the notothyrial platform.
Up. Cambrian, S. side Gallatin Valley, Mont. U. S. Nat. Mus. x 2.

Eoorthis cf. remnicha (Winchell)

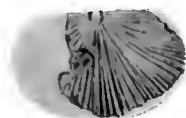
- 26.—Ventral interior, showing thickening on floor of delthyrial cavity. This type of structure is called a pseudospondylium, but the resemblance to a spondylium is very remote in *Billingsella* and *Eoorthis*.
- 28.—Dorsal interior, showing flat, oblique brachiophores. This specimen is deprived of a cardinal process, hence the muscles were attached on the floor of the notothyrial cavity.
Up. Cambrian, Flat River, Mo. U. S. Nat. Mus. x 2.

Jamesella cf. perpasta (Pompeckj)

- 24.—Ventral internal mold of a large specimen, showing muscular marks.
Up. Cambrian, Skrej, Bohemia. Cat. No. S 1944. x 2.



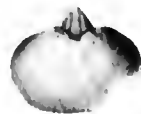
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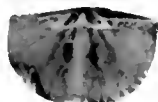
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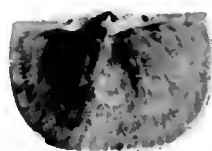
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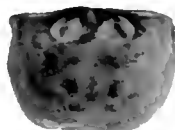
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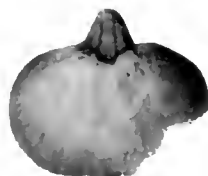
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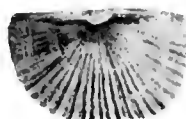
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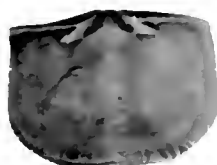
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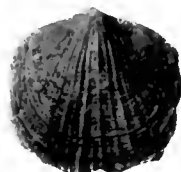
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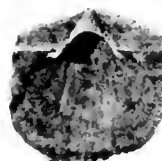
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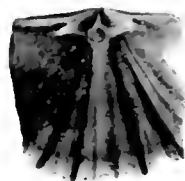
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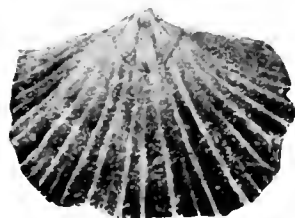
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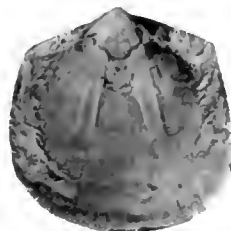
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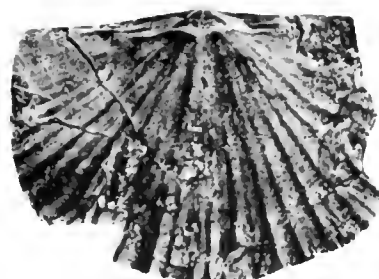
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PLATE 2

FIGS. *Nicolella* cf. *actoniae* (Sowerby)

- 1, 3.—Dorsal and ventral views of a well preserved individual. Cleft chilidium, or chilidial plates, visible in fig. 1. Compare angular costæ and predominantly concentric finer ornamentation with those of *Orthis* (figs. 9, 11, 12, 15).
Ordovician (Lyckholm, F₁), Piersal, Estonia. Cat. No. S 151. x 2.

Nicolella actoniae (Sowerby)

- 4, 6.—Dorsal and ventral views of a large specimen, showing anterior bifurcation of costæ.
5.—Ventral internal mold, showing muscle impressions.
Ordovician (Chasmops ls.), Ostragothia, Sodra Freberga, Sweden. Cat. No. S 152. x 2.

Nicolella, n. sp.

- 2.—Dorsal view of a specimen related to *N. moneta* (Eichw.), showing coarse angular costæ.
Ordovician (Wierland group, Echinosphærites ls.), Popovka near Leningrad, Russia. Cat. No. S 147. x 2.65.

Orthis cf. *calligramma* Dalman

- 7, 9, 11, 13.—Posterior, dorsal, ventral, and lateral views of the same specimen. Note biconvexity of shells, rounded costæ, and parvicostellæ in the striæ.
Middle Ordovician, Pulkova, near Leningrad, Russia. Cat. No. S 167. x 2.

Orthis rotunda Pander

- 10.—Dorsal interior, showing simple brachiophores, septum-like cardinal process, small adductor impressions, and pallial sinuses radiating from them. The sockets for the teeth are the space between the brachiophores and the wall of the valve.
Ordovician (Walchow), opposite Iswos, Russia. Mus. Comp. Zool., Harvard Coll. x 2.

FIGS. *Orthis rotunda* Pander—*Cont.*

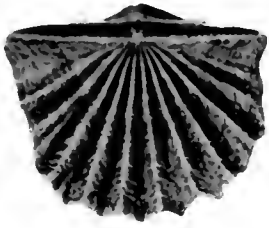
- 16.—Dorsal interior, showing median ridge and pallial markings.
18.—Ventral interior, showing two prominent pallial trunks, closely apposed and separated by a small, low ridge. These trunks bound, on the inside, subreniform ovarian markings. It is this type of interior that characterizes the ventral valve of the *Orthidæ* as here conceived.
Ordovician (Walchow), opposite Iswos, Russia. Mus. Comp. Zool., Harvard Coll. x 2.

Orthis callactis Dalman

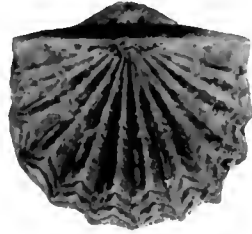
- 8, 12, 15.—Posterior, ventral, and dorsal views of the same individual. Coarse, simple, rounded ribs covered by fine radii and finer concentric growth markings clearly visible. *O. callactis* is the type of the genus *Orthis*, and the kind of shell to which this generic name should be restricted. Compare the outline and contour with those of *O. calligramma* (figs. 7, 9, 11, 13). A critical study of large collections of European *Orthis* may prove the advisability of separating the *O. calligramma* type as a subgenus.
Ordovician (Walchow, Glauconite ls.), Iswos, Walchow River, Russia. Cat. No. S 144. x 2.
17.—Dorsal interior, showing small, simple brachiophores. Ordovician, opposite Iswos, Russia. Shaler Mem. Exped. Colls., Mus. Comp. Zool., Harvard Coll. x 2.

Cyrtotonotella aff. *C. frechi* (Wysogorsky)

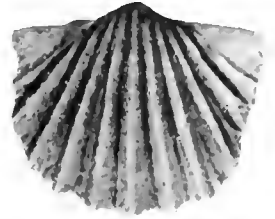
- 14.—A kind of biconvex *Orthis* with prominent concentric lines covering the costæ.
Ordovician (Echinosphærites ls., C), Popovka, near Leningrad, Russia. Cat. No. S 2099. x 2.



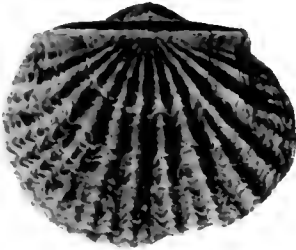
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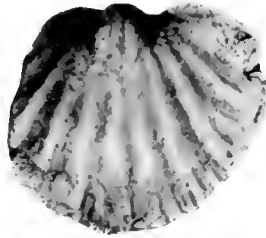
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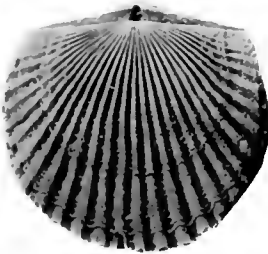
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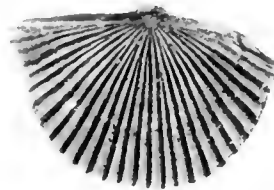
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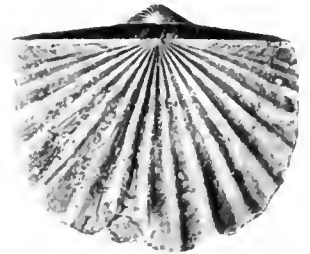
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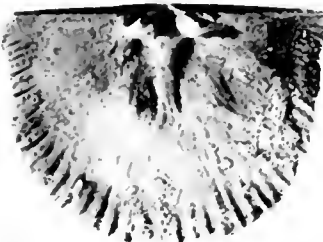
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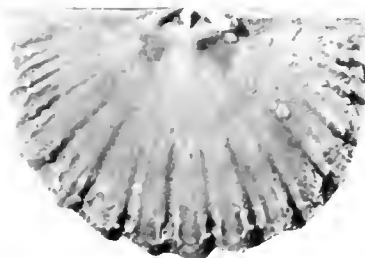
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PLATE 3

FIGS. *Panderina abscissa* (Pander)

- 1, 4.—Dorsal and ventral views of a specimen belonging to the genotype, showing characteristic ornamentation, especially concentration of growth toward the front. Note reduced (shortened) ventral interarea well shown in fig. 1.

Ordovician (Glaconite ss.), Popovka, near Leningrad, Russia. Cat. No. S 157. x 2.25.

Panderina tetragonum (Pander)

- 2, 3.—Dorsal and ventral interiors. After Lamansky, Mém. Com. Géol., 1905, pl. 2, figs. 11, 12.

Ordovician (Walchow, B₁β), Popovka, near Leningrad, Russia. Slightly enlarged.

Paurorthis parva (Pander)

- 5.—Ventral interior, showing teeth, crural fossettes, median ridge, and lateral ovarian areas. The muscle area shows a broad adductor-diductor impression. Cf. *Dalmanella rogata*, pl. 17, fig. 4.
- 7.—Dorsal interior, showing subradial pallial sinuses, indistinct muscle field, and prominent elevated median ridge. Brachiophores oblique, divergent plates supported by a swelling of adventitious tissue, to be seen at posterior portion of median ridge. Cardinal process a faintly discernible ridge just behind the swelling of adventitious substance. Cf. *Dalmanella rogata*, pl. 17, fig. 31.
- 8, 10.—Ventral and dorsal exteriors of a large individual. Note reduced (shortened) ventral interarea and subfasciculate costellæ. The general external resemblance of *P. parva* to *Dalmanella* is a striking instance of homœomorphy. *Paurorthis*, however, differs internally as illustrated above (figs. 5, 7). It differs also in being impunctate (no endopunctæ) but possesses numerous exopunctæ which have led to its misidentification as *Dalmanella*.

Ordovician (Glaconite ls.), Gornaja Scheldicha, Lake Ladoga, Russia. Cat. No. S 136. x 3.

- 6.—Ventral interior, showing broad pallial trunks separated by a low median ridge. Subreniform ovarian areas occupy lateral portions of valve. Wide adductor-diductor track clearly visible and adjustor (?) impressions outside these may be seen. The interior of

FIGS. *Paurorthis parva* (Pander)—Cont.

Paurorthis is thus close to that of *Orthis* s. s., and the genus forms a remarkable homœomorph of *Dalmanella* s. s.

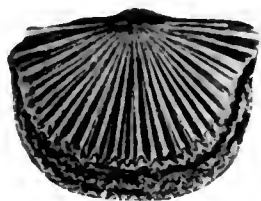
Ordovician, opposite Isvos, Russia. Shaler Mem. Exped. Colls., Mus. Comp. Zool., Harvard Coll. x 3.

Productorthis parallela (Pander)

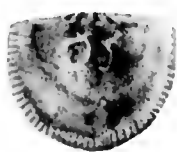
- 9.—Ventral interior, showing reduced (shortened) interarea, prominent dental plates, and peculiar muscle field. The small, elliptical impressions at the base of the dental plates have usually been interpreted as diductor scars; they are, however, smaller than is common for the scars of the diductors and probably represent adjustor muscle impressions. The diductor-adductor impressions occupy the large central elevated area.
- 13, 16.—Ventral and dorsal exteriors, showing imbricating lamellæ or "ruffles," remarkable "productoid" form, and nearly obsolete interareas.
- Ordovician (Chazy, Glaconite ls.), Gornaja Scheldicha, Lake Ladoga, Russia. Cat. No. S 126. x 3.
- 11.—Dorsal interior, showing elongated cardinal process with its compressed myophore. The brachiophores have developed into cuplike structures which receive large teeth. Circular chilidium visible on dorsal surface of free or posterior end of cardinal process. Bipartite character of anterior adductor impressions clearly visible. The ribbed elevated border around the periphery of the shell is an aid in articulation.
- 12.—Reverse, or dorsal, surface of fig. 11, showing imbricated exterior and small, umbrella-like chilidium covering free end of cardinal process.
- Ordovician (Chazy, Glaconite ls., B₂), Popovka, near Leningrad, Russia. Cat. No. S 127. x 3.

Productorthis cf. *eminens* (Pander)

- 14, 15.—Ventral and dorsal exteriors of a species having finer ribbing. The "ruffled" exterior, however, is well exhibited. In fig. 15, ventral interarea nearly obsolete, and a rounded foramen formed by resorption of the beak by the pedicle.
- Ordovician (Glaconite ls., B₃), Popovka, near Leningrad, Russia. Cat. No. S 122. x 3.



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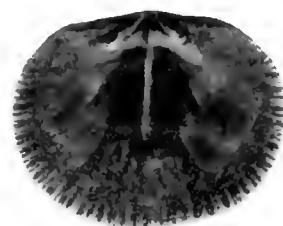
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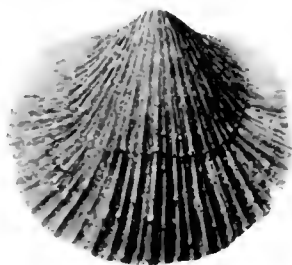
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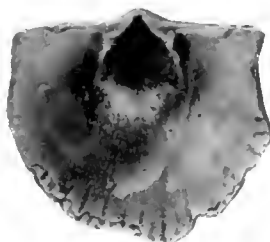
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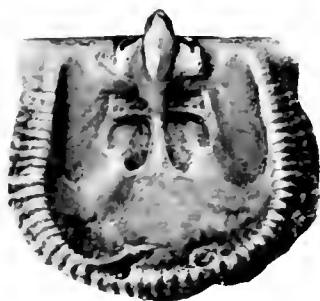
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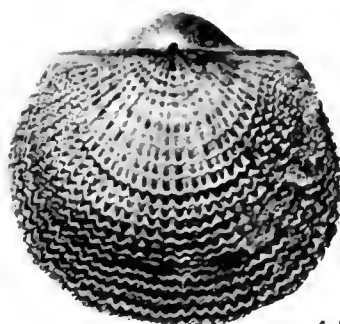
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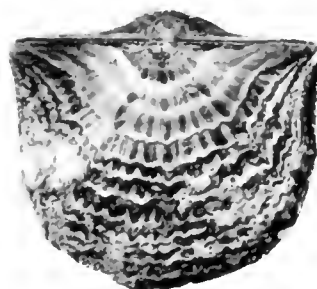
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PLATE 4

FIGS. *Cyrtonotella semicircularis* (Eichwald)

- 1, 4, 5, 11.—Ventral, dorsal, posterior, and lateral views, showing multicostate exterior, short interarea, and concave dorsal valve.
Ordovician (Echinosphaerites ls.), Popovka, near Leningrad, Russia. Cat. No. S 169. x 5.

Glossorthis tacens Öpik

- 2, 8.—External and internal views of the same dorsal valve. The latter illustrates the cardinal process and the thickening or swelling just in front of it that supports the brachiophores. The latter structures are broken off near the sockets so that their full length is not revealed. Anterior adductor scars bipartite as in *Productorthis* and many other orthoid genera.
7, 9.—External and internal views of an exceptionally well preserved ventral valve. Fig. 9 illustrates well the pseudospondylium and also the various muscle impressions. This pseudospondylium is entirely a secondary feature, being best developed in mature shells, and is formed as a deposit under the muscle attachments. In *G. extensa*, the pseudospondylium is not developed to such a marked degree. For details of the ventral interarea, see fig. 28.
12.—Ventral valve, tilted upward to afford a better view of the pseudospondylium. The short septum visible in front, and the thick rim, are adventitious deposits simulating a spondylium.
28.—Enlarged view of interarea of ventral valve of the same specimen illustrated in fig. 9, x 3, showing ponderous teeth and heavy lateral (deltidial?) plates along delthyrial margin. On the right side of the delthyrium, one of these is well shown, the suture being emphasized by slight fracturing.
Mid. Ordovician (C₂), Kohtla, Estonia. Cat. No. S 2100. All except fig. 28 x 1.5.

Glossorthis extensa (Verneuil non Pander)

- 3, 6, 10.—Dorsal, posterior, and lateral views of the same individual.
Ordovician (Glaucinite ls., B₂), Popovka, near Leningrad, Russia. Cat. No. S 161. x 1.5.

Productorthis parallela (Pander)

- 15, 16.—Internal and external views of posterior of the same individual as in pl. 3, figs. 11, 12. Note unusual cardinal process and cuplike adventitious shell supporting brachiophore in fig. 15, and umbrella-like chilidium in fig. 16.
Ordovician (Glaucinite ls., B₂), Popovka, near Leningrad, Russia. Cat. No. S 127. x 3.

FIGS. *Hesperorthis tricenaria* (Conrad)

- 13, 14, 25.—Ventral, dorsal, and posterior views of a complete individual. Contrast broad interareas of figs. 14 and 25 with shortened ones of *Orthis*, figs. 7 and 8 of pl. 2.
26.—Smaller specimen preserving remnantal chilidium and deltidium.
Ordovician (Black River), Cannon Falls, Minn. Cat. No. S 199. x 1.5.
17.—Internal view of dorsal valve, showing chilidium, brachiophores, strong median elevation, and internal marginal ribbing. This type of marginal ribbing, with a cleft internal rib corresponding to the stria (groove) of the exterior, is common to many genera of the Orthidæ. x 2.
18.—Same shell, tipped forward to give a better view of the convex chilidium. x 2.
29.—Enlargement (x 4) of cardinalia of fig. 18, to show chilidium and brachiophores in greater detail. These brachiophores are typical of the "*Orthis*" type, long and pointed, grooved on the inside, triangular in section, the outer sloping face forming resting places for the teeth of the ventral valve, the crural fossette of the ventral tooth resting on the carinate, postero-ventral ridge of the brachiophores.
Ordovician (Trenton), St. Paul, Minn. Cat. No. S 210.
19, 27.—Ventral interiors, showing long interarea and short deltidium. Notice distinct suture-lines between margins of delthyrium and deltidium. In fig. 27 the slender ridge dividing the main pallial trunks of the ventral valve is visible, and a few of the elevated lines of the ovarian areas can be seen near the hinge margins.
21.—Dorsal interior, showing cardinal process and brachiophores. Anterior portion of the cardinal process bearing a shallow groove.
Ordovician (Trenton), Scullsbury, Wis. Cat. No. S 176. Fig. 19 x 1.5; figs. 21 and 27 x 2.
20.—Ventral valve, showing details of interarea. This specimen illustrates a feature of unusual interest: the delthyrium is extremely narrow, having been diminished by the growth of marginal plates inside the teeth. (See fig. 28.) Deltidial plate an arch under delthyrial margins.
Ordovician (Black River), Minneapolis, Minn. Cat. No. S 2101. x 1.5.

Hesperorthis davidsoni (Verneuil)

- 22, 23.—Dorsal and ventral exteriors of a well preserved individual. In fig. 22 perforations are visible on the surface of the costæ, but these external apertures are not to be confused with punctæ (endopunctæ).
24.—Dorsal interior, showing muscle-scars and cardinalia.
Silurian (Gotlandian), Gotland, Sweden. Cat. Nos. S 203, S 204 (fig. 24). x 1.5.

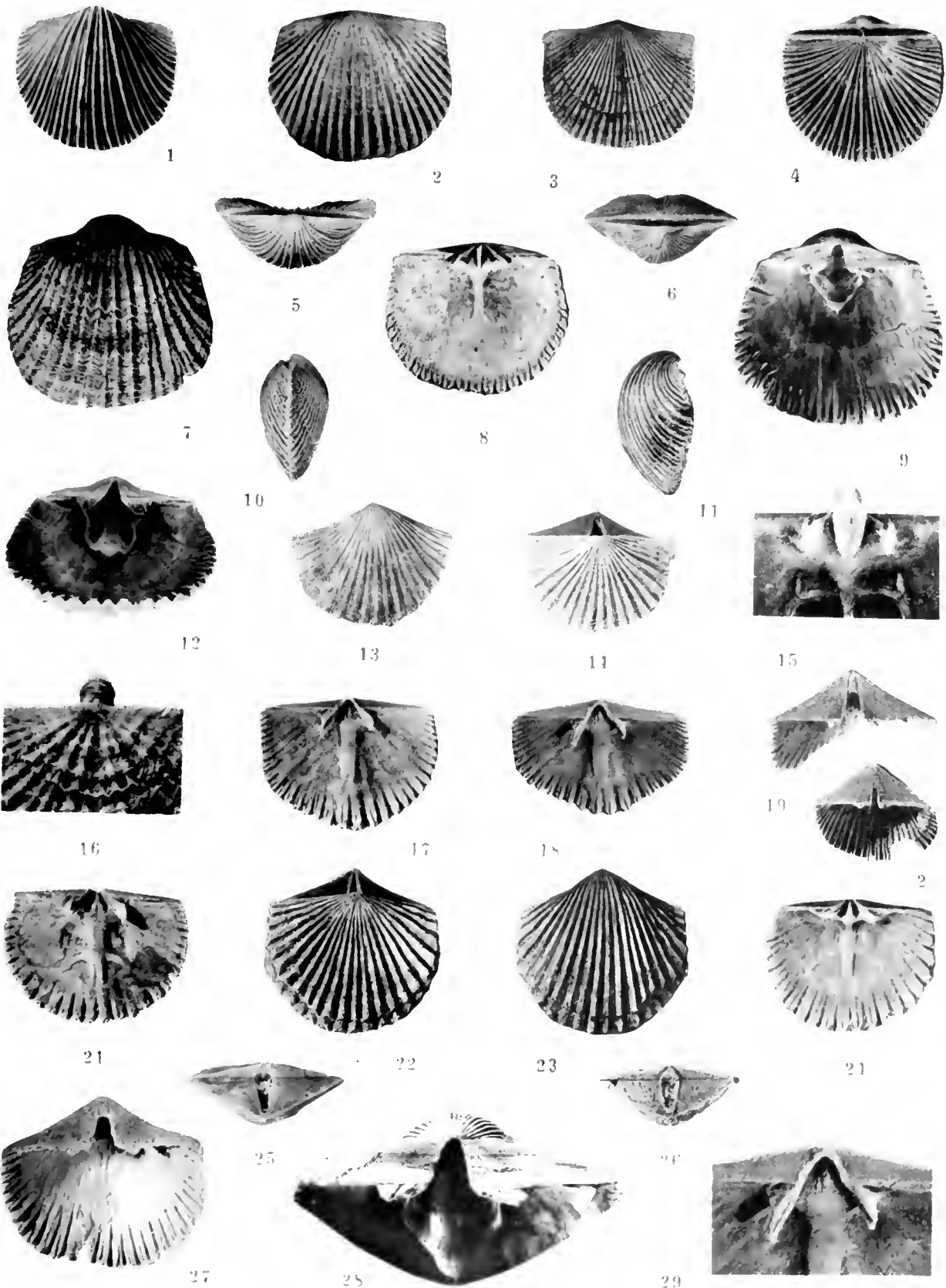


PLATE 5

FIGS. *Eridorthis rogersensis* Foerste

- 1, 5.—Dorsal exteriors, showing fold. In early stages the dorsal valve bears a sulcus which later reverses and becomes a fold.
Ordovician (Trenton, Cynthiana), Rogers Gap, Ky.
Cat. No. 78712, U. S. Nat. Mus. x 1.5.

Eridorthis aff. *E. nicklesi* Foerste

- 2.—Ventral internal mold, showing *Orthis*-like musculature, pallial trunks, and low median rib.
Ordovician (Eden, Fulton), New Richmond, Ohio.
Cat. No. S 2102. x 2.

Eridorthis nicklesi Foerste

- 9.—Ventral valve, showing depression of fold to form a sulcus at front of valve.
Ordovician (Trenton, Cynthiana), Rogers Gap, Ky. Cat. No. 78711 U. S. Nat. Mus. x 1.5.

Glyptorthis fausta (Foerste)

- 4.—Dorsal interior, showing *Hesperorthis*-like cardinalia.
7.—Ventral interior, illustrating musculature of the genus.
Silurian (Brassfield), near Dayton, Ohio. Cat. No. S 236. x 1.5.
8.—Dorsal exterior, showing incipient sulcus at posterior.
Silurian (Brassfield), Centerville, Ohio. Cat. No. S 238. x 1.5.

Schizoramma ? *gotlandica* Schuchert and Cooper, n. sp.

- 3, 6.—Dorsal and ventral exteriors.
Silurian (Gotlandian), Gotland, Sweden. Cotypes.
Cat. No. S 228. x 1.5.

Schizoramma nisis (Hall and Whitfield)

- 11, 16.—Ventral and dorsal exteriors of a silicified specimen, showing ornamentation.
Silurian (Niagaran, Meniscus), W. Tennessee. Cat. No. S 221. Fig. 11 x 1.5; fig. 16 x 2.

Schizoramma fasciata (Hall)

- 13.—Ventral interior, somewhat crushed, showing orthoid musculature, and, more indistinctly, the two closely apposed pallial trunks.
14.—Dorsal interior, to show orthoid brachiophores; low, broad, median ridge; simple cardinal process; and accessory ridges on each side of it. Small adductor impressions more indistinctly visible.
Silurian (Clinton), Osgood, Ind. Cat. No. S 222. x 1.5.

FIGS. *Schizoramma fasciata* (Hall)—Cont.

This genus has been described as a subgenus of *Orthostrophia*, but from its internal structure is distinct enough to merit generic rank. *Schizoramma* does not have the small, confined ventral muscle area and the elevated adductor impressions of the other genus.

Dolerorthis rustica osiliensis (Schrenk)

- 10, 12, 19, 21.—Lateral, posterior, dorsal, and ventral views of exterior, fig. 10 showing faint concavity of ventral valve toward the front.
15.—Dorsal interior, showing orthoid brachiophores and cardinal process, and notothyrial platform.
Silurian (Gotlandian), Gotland, Sweden. Cat. No. S 282. x 1.5.
20.—Ventral interior, showing closely apposed pallial trunks separated by a low septum that forks at the front. Subreniform ovarian impressions bounded by these sinuses. Compare with *Orthis* s. s., *Hesperorthis*, and *Glyptorthis* (pl. 2, fig. 18; pl. 4, fig. 27; pl. 6, fig. 26).
23.—Dorsal interior, showing median ridge, orthoid cardinalia, large posterior adductor scars, and smaller bipartite anterior adductor impressions. Cf. fig. 24.
Silurian (Wenlock), England. Mus. Comp. Zool., Harvard Coll. x 1.5.

Dolerorthis interplicata (Foerste)

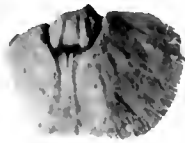
- 18.—Dorsal interior, showing characteristic cardinalia.
Silurian (Niagaran, Osgood), Osgood, Ind. Cat. No. S 279. x 1.5.

Dolerorthis flabellites (Foerste)

- 17, 24.—Obese dorsal interiors, illustrating interesting old-age modifications of cardinalia and notothyrial platform, and brachiophores heavily overgrown with adventitious shell substance, which hides them almost completely. Note "orthoid" ribbing of internal margin. In fig. 24, note especially adductor impressions and compare with fig. 23. Compare fig. 24 with fig. 8 of pl. 1.
22.—Ventral interior, showing orthoid musculature, and pallial sinuses bounding subreniform ovarian impressions. Cf. fig. 20, and ventral interiors of *Orthis*, *Hesperorthis*, and *Glyptorthis*.
Silurian (Niagaran, Osgood), Osgood, Ind. Cat. No. S 272. x 1.5.



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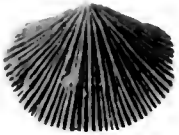
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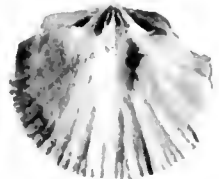
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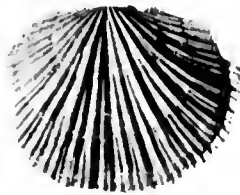
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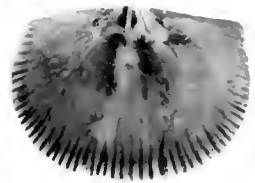
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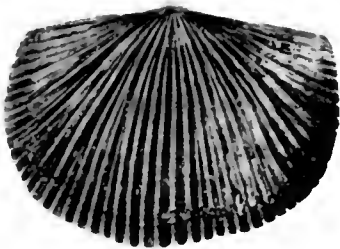
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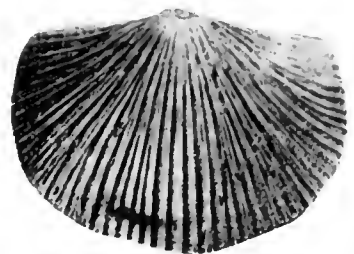
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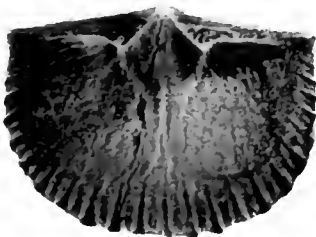
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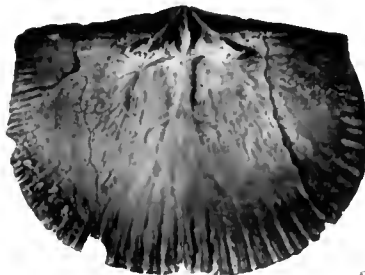
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PLATE 6

FIGS. *Ptychopleurella bouchardi* (Davidson)

- 1, 33.—Ventral interiors, showing musculature, pedicle callist, and median ridge.
 - 3, 4.—Ventral and dorsal exteriors, showing prominent costæ and lamellose exterior.
 - 6, 32.—Dorsal interiors, showing cardinal process, brachio-phores, and adductor impressions.
- Silurian (Gotlandian), Gotland, Sweden. Cat. No. S 285. Figs. 1, 3, 4, 6 x 2; figs. 32, 33 x 3.

Ptychopleurella matapedia Schuchert and Cooper, n. sp.

- 2, 5.—Dorsal and ventral exteriors of a silicified specimen, showing strongly lamellose surface.
- High Silurian or basal Devonian, Upsalquitch road, Matapedia, Quebec. Holotype. Cat. No. S 287. x 2.

Ptychopleurella lamellosa (Twenhofel)

- 9.—Posterior view of holotype, showing slitlike delthyrium produced by growth of lateral plates.
- Ordovician (Ellis Bay), Ellis Bay, Anticosti. Cat. No. 10411 Y. P. M. x 5.

Archæorthis electra (Billings)

- 7.—Ventral exterior. x 2.
 - 8.—Ventral interior, showing callus extending forward from muscular area.
 - 16.—Dorsal interior, showing low median ridge, nearly obsolete cardinal process, and brachio-phores. x 4.
- Ordovician (Canadian), Levis, Quebec. Cat. No. 740, Nat. Mus. Canada. All silicified.

Deltatrete typica Ulrich MS.

- 10, 19.—Dorsal and ventral exteriors, x 1.5, showing costellate exterior and hollow costellæ.
 - 14.—Portion of a silicified ventral valve, x 3, showing deltidium and large, subapical foramen. Faint radial lines also visible on interarea.
 - 30.—Silicified dorsal interior, x 2.25, with a ventral valve lying in it. Primitive nature of brachio-phores and their lateral supports like those of *Vellamo* plainly shown, also simple cardinal process and chilidial plates projecting posteriorly from notothyrial margin. The ventral interior shows well the pedicle callist.
- Ordovician (up. Canadian, ca. 1000 feet beneath top of Arbuckle ls. (formation name not yet given)), near Berwyn, Okla. (U. S. G. S. loc. 191K). U. S. G. S. colls., U. S. Nat. Mus.

Deltatrete sp.

- 15.—Ventral interior, showing prominent dental plates and pseudospondylium, the latter produced by a deposit of adventitious shell beneath the muscles. Cf. ventral interior in fig. 30; cf. also fig. 13.
- Ordovician (2d Ceratopea zone), "inlier," sect. 25, T 6 N, R 14 W, N. E. of Wichita Mts., Okla. U. S. Nat. Mus. x 2.

FIGS. *Deltatrete dice* (Walcott)

- 11.—Dorsal interior, showing primitive cardinalia.
 - 13.—Ventral interior, showing pseudospondylium. Cf. fig. 15.
- Drift (probably Ordovician (Canadian)), St. Albans, Vt. Impressions from type specimens, U. S. Nat. Mus. Cat. No. 52248. x 1.5.

Glyptorthis cf. *bellarugosa* (Conrad)

- 12.—Dorsal exterior, showing lamellose surface.
- Ordovician ("Simpson"), Criner Hills, Okla. Cat. No. S 251. x 2.

Glyptorthis insculpta (Hall)

- 17, 20, 21.—Ventral, dorsal, and lateral views of exterior. Lateral profile biconvex. Cf. same view of *Hebertella*, pl. 11, fig. 19.
- 18, 26.—Ventral interiors, showing "Orthis" pattern to perfection. Note muscle area; central adductor track straight, diductor tracks elongate tear-shaped; and adjustor scars visible at base of dental plates. Extending forward from the adductor track is a low septum which divides the closely apposed pallial sinuses originating at the front ends of the diductor impressions. Lateral spaces occupied by subreniform ovarian impressions. Elevated lines in these impressions considered to be muscle attachments for ovarian bodies.
- 29.—Dorsal interior, showing an old shell heavily ridged by pallial markings. Note adductor scars. The cardinalia of *Glyptorthis* are of the "Orthis" type, differing markedly from those of *Hebertella*. See pl. 11, figs. 24, 26.

Glyptorthis has been usually considered to be a subgenus of *Hebertella*, but its lenticular profile and internal structure relate it rather to *Hesperorthis* and *Orthis*. Ordovician (Richmond), Oxford, Ohio. Cat. No. S 242. x 1.5.

Orthostrophia strophomenoides (Hall)

- 22.—Dorsal internal mold, showing muscle area and pallial markings.
 - 25.—Impression from the above, showing elevated muscle area.
- Devonian (New Scotland), near Clarksville, N. Y. Cat. No. S 320. x 2.
- 27, 28.—Ventral and dorsal exteriors, showing characteristic ornamentation.
- Devonian (Birdsong), Henry Co., Tenn. Cat. No. 9702 Y. P. M. x 1.

Orthostrophia aff. *O. strophomenoides* (Hall)

- 24.—Ventral internal mold, showing small muscle area and pallial markings.
- Devonian (Hunton), near Crusher, Okla. Cat. No. S 322. x 1.5.

Orthostrophia dartæ Schuchert and Cooper, n. sp.

- 23.—Ventral internal mold of paratype, showing small muscle area.
 - 31.—Dorsal exterior of holotype, showing ornamentation.
- Silurian (Bouleaux), Port Daniel, Quebec. Cat. No. S 1985. x 1.5.

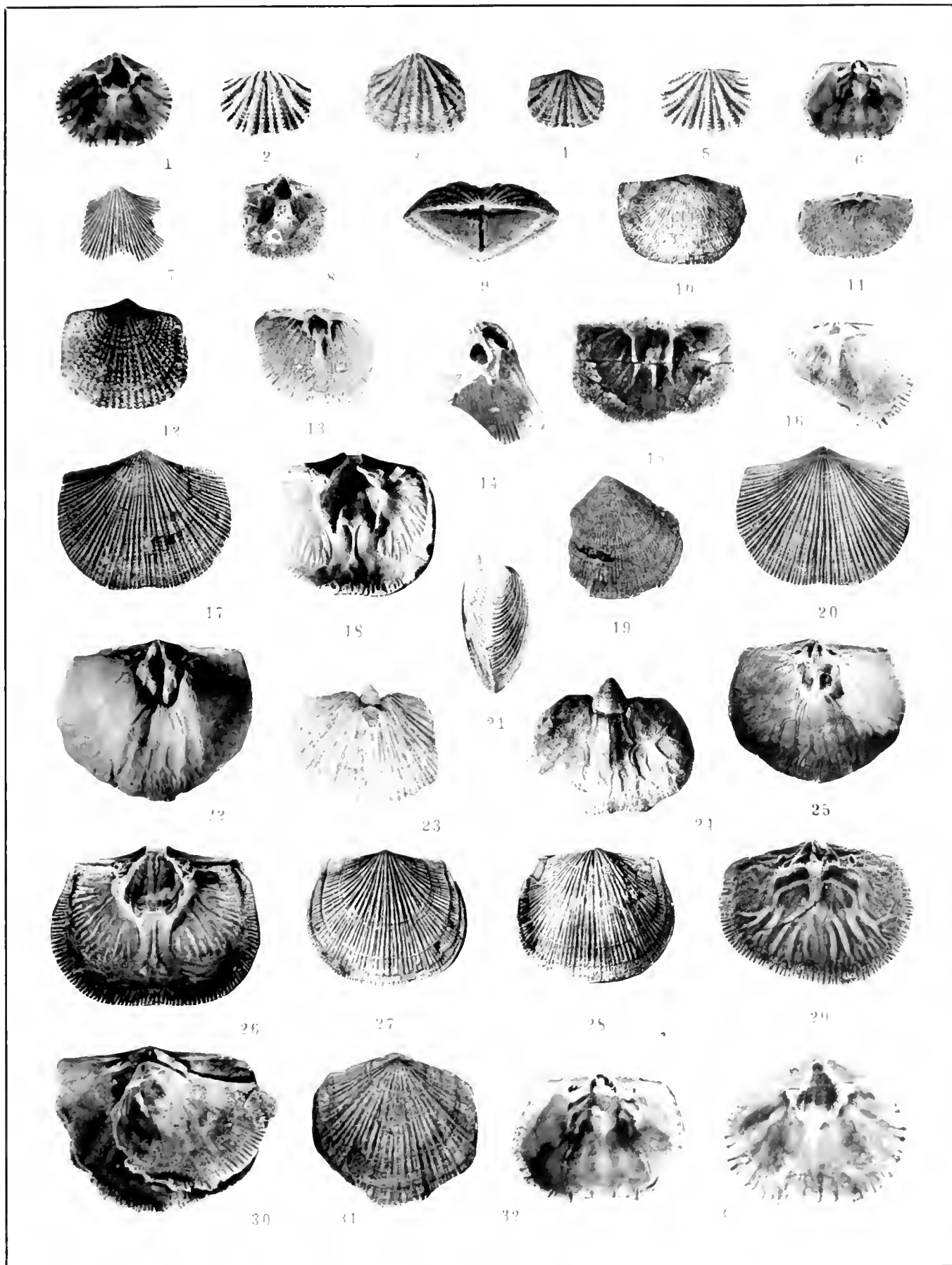


PLATE 7

FIGS. *Pahlenella trigonula* (Eichwald)

- 1, 3.—Ventral and dorsal exteriors. Dorsal valve concave.
 2.—Ventral interior, showing deltidium and sessile spondylium.
 4.—Dorsal interior, showing short brachiophores, chlidium, and elevated muscle area.
 Ordovician (Canadian, Walchow, B₂), Popovka, near Leningrad, Russia. Cat. No. S 370. x 2.

Aff. *Vellamo multicosta* (Hudson)

- 5, 11.—Views of the same ventral interior, showing remnant of imperforate deltidium.
 8.—Ventral interior, showing septum dividing two closely apposed pallial trunks, and, outside these, ovarian areas as in *Glyptorthis* et al.
 9.—Dorsal interior, showing cardinalia and musculature.
 10.—Ventral interior, showing muscle impressions on spondylium.

These shells are doubtfully referred to *Vellamo*, differing from that genus in having what appears to be an imperforate deltidium, and in details of the dorsal valve.

Ordovician (Chazy), Sloop Bay, Valcour Island, N. Y. Cat. No. S 359. x 2.

Vellamo trentonensis (Raymond)

- 14.—Ventral interior, showing spondylium and its supporting septum, and deltidium.
 28.—View of interarea and deltidium. Note position of teeth.
 Ordovician (Galena, bed 6), Kenyon, Minn. Cat. No. S 342. x 1.5.
 18.—Dorsal interior, showing anchor-shaped cardinalia and musculature.
 Ordovician (Galena), Cannon Falls, Minn. Cat. No. S 348. x 1.5.

Cf. *Vellamo squamata* (Pahlen)

- 15.—Interarea.
 31.—Interior, showing spondylium.
 Ordovician (C₂), Kohtla, Estonia. Cat. No. S 2105. x 1.5.

FIGS. *Vellamo* cf. *emarginata* (Pahlen)

- 16, 29, 30, 32.—Posterior, ventral, lateral, and dorsal views of the same individual, showing details of ornamentation and contour and outline of valve.
 Ordovician (Mohawkian, Wesenberg), Wesenberg quarries, Estonia. Cat. No. S 339. x 1.5.

Vellamo verneuili (Eichwald)

- 24, 27.—Dorsal and ventral exteriors of type species of genus.
 Ordovician (Cincinnatian, Lyckholm, F₁), Kertel, Estonia. Cat. No. S 347. x 1.5.

Vellamo diversa (Shaler)

- 25.—Dorsal interior, showing cardinalia and musculature.
 Ordovician (Ellis Bay), Junction Cliff, Anticosti. Cat. No. 10335 Y. P. M. x 1.5.

Apomatella ingrica (Pahlen)

- 6, 7.—Views showing spondylium.
 12.—Ventral exterior, showing also dorsal valve in conjunction.
 13.—Ventral exterior, showing procline position of interarea.
 These shells may be somewhat remote from the true *Vellamo* line.
 Ordovician (Canadian, Walchow, B₂), Popovka, near Leningrad, Russia. Cat. No. S 2104. x 2.

Clitambonites adscendens (Pander)

- 17, 19, 22, 23.—Posterior, dorsal, ventral, and lateral views of exterior. Note particularly ornamentation and procline interarea. Deltidium commonly imperforate in adult shells. x 1.5.
 20, 21.—Ventral and dorsal interiors, the former showing the spondylium. Note peripheral border or frill. x 1.5.
 26.—Enlargement of exterior of specimen in fig. 19, x ca. 4.5.
 Ordovician (Canadian, Kunda), Popovka, near Leningrad, Russia. Cat. No. S 372.

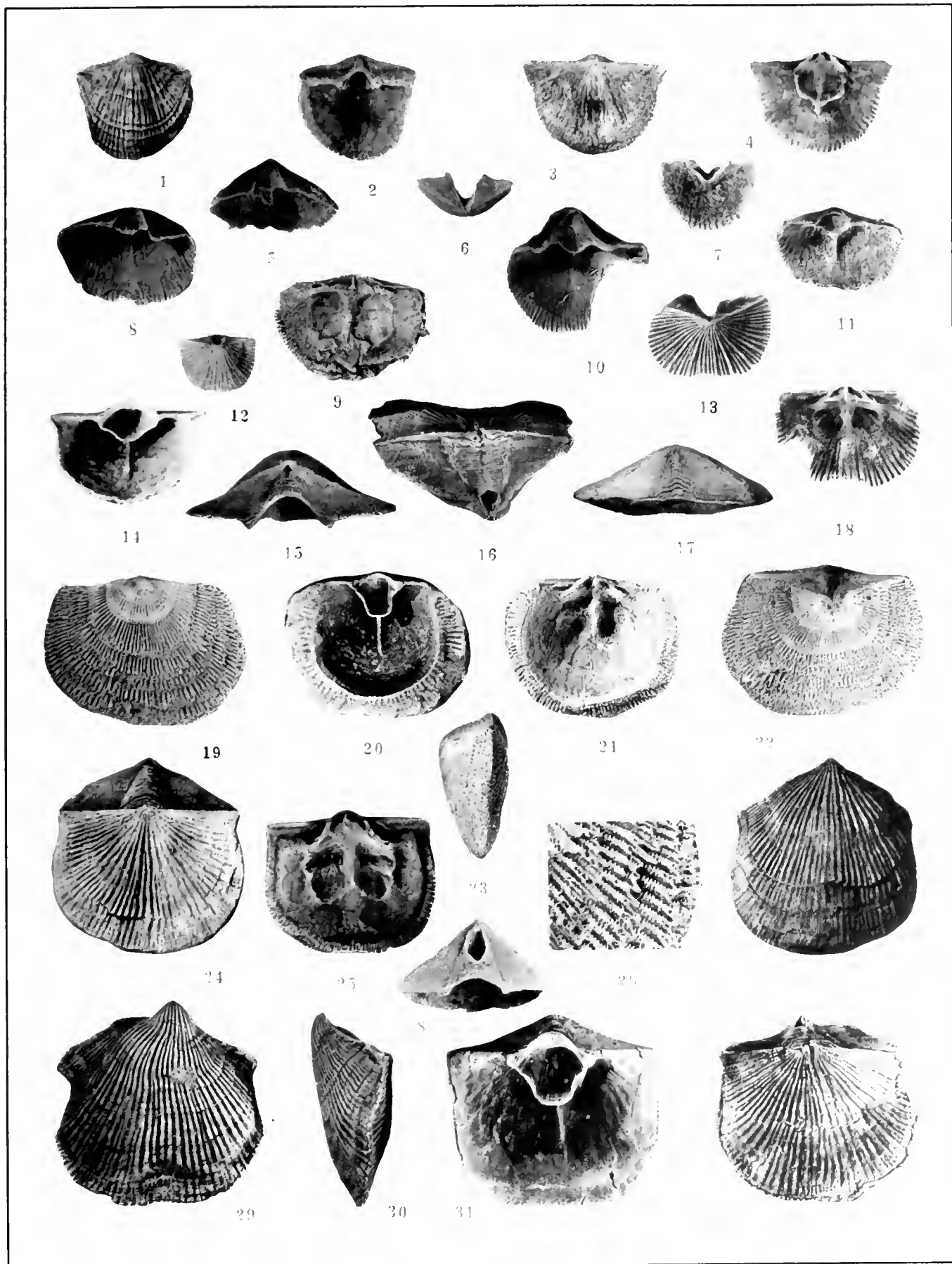


PLATE 8

FIGS. *Gonambonites planus* Pander emend. Pahlen

- 1.—Ventral interior, showing spondylium and its accessory septa. Marginal thickening visible also.
- 2, 3, 20.—Dorsal, ventral, and posterior views of a small individual, showing prominent process extending from deltidium. Fig. 20 shows deltidium somewhat crushed in.
- 4, 7.—Dorsal interiors, showing cardinalia and chilidial plates. Brachiophores to be seen protruding from lateral adventitious thickening just antero-laterally of notothyrium.
- 5, 21, 26.—Posterior, ventral, and dorsal views of a large shell, showing characteristic ornamentation.
Ordovician (Canadian, Walchow, B₂), Wassilkowo, near Lake Ladoga, Russia. Cat. No. S 333. x 1.5.
- 25.—Ventral interior of a large specimen.
Same locality as above. Shaler Mem. Exped. Colls., Mus. Comp. Zool., Harvard Coll. x 1.5.

Estlandia marginata (Pahlen)

- 6.—Dorsal interior, showing cardinalia and median ridge. Brachiophores may be seen in postero-lateral portions of shell just outside adventitious thickenings anterior and laterally of notothyrium.
- 8.—Ventral interior, showing spondylium. Foramen in deltidium closed by a plug of shell substance.
Ordovician (Kuckers, Brandschiefer), Baron Toll's estate, near Jewe, Estonia. Cat. No. S 327. x 1.5.
- 9.—A fine dorsal interior, showing cardinalia. Notice brachiophores outside anchor-shaped adventitious deposits.
Middle Ordovician (C_{3a}), Kohtla, Estonia. Cat. No. S 2106. x 1.5. Presented by A. Öpik.

Hemipronites tumidus Pander

- 10.—Ventral interior with deltidium missing, showing median septum dividing two pallial trunks which in turn surround inside margins of subreniform ovarian impressions. Cf. *Glyptorthis insculpta*, pl. 6, figs. 18, 26, and *Orthis*, pl. 2, fig. 18. It will be noted that the spondylium is the homologue of the dental plates and floor of the deltidial cavity. The septum is the homologue of the small ridge dividing the pallial sinuses in *Orthis s.s.*; the sinuses are situated in precisely the same place and bound similar ovarian impressions.
Ordovician (Walchow, B₂), Popovka, near Leningrad, Russia. Cat. No. S 369. x 1.5.

FIGS. *Hemipronites tumidus* Pander—Cont.

- 11.—Dorsal interior, showing cardinalia. Cardinal process simple as in *Orthis s. s.*, and brachiophores rodlike plates supported by adventitious tissue which, in this instance, spreads laterally to form an anchor-shaped mass with the median ridge.
- 14, 15.—Posterior and ventral exteriors, showing ornamentation.
Ordovician (Walchow, B₂), Popovka, near Leningrad, Russia. Cat. No. S 369. x 1.5.

Hemipronites cf. maximus Pander

- 12, 13.—Ventral and dorsal exteriors, showing fine costellæ.
Ordovician (Canadian, Walchow), Popovka, near Leningrad, Russia. Cat. No. S 365. x 1.

Marionella typa Bancroft

- 16.—Dorsal internal mold, showing dinorthis character of cardinalia.
- 17.—Muscle-scars and pallial markings of ventral valve.
- 18.—Impression showing external sculpture.
Ordovician (upper Longvillian), Horderley District, East Shropshire, England. Cat. No. S 2107 (fig. 18), and S 2108. x 1.5.

Multicostella platys (Billings)

- 19, 23.—Ventral and dorsal exteriors, showing ornamentation of this biconvex dinorthis.
Ordovician (Chazy), Speer's Ferry, Virginia. Cat. No. S 92. x 1.5.

Multicostella saffordi (Hall and Clarke)

- 22.—Ventral interior, showing musculature, which is similar to that of *Valcourea*.
- 27.—Dorsal interior, with crenulated dinorthis cardinal process plainly visible. Brachiophores also similar to those of *Valcourea*.
Multicostella was common in Chazy time, but evidently did not survive this stage. A deltidium or chilidium is unknown in this dinorthis stock.
Ordovician (Chazy), Washburn, Tenn. Cat. No. S 786. x 1.5.

Clinambon anomalus (Schlotheim)

- 24, 28.—Posterior and lateral views, showing unusual development of chilidium, and posterior portion of dorsal valve.
Ordovician (Mohawkian, Kegel, D₂), Kedder, Estonia. Cat. No. S 337. x 1.5.

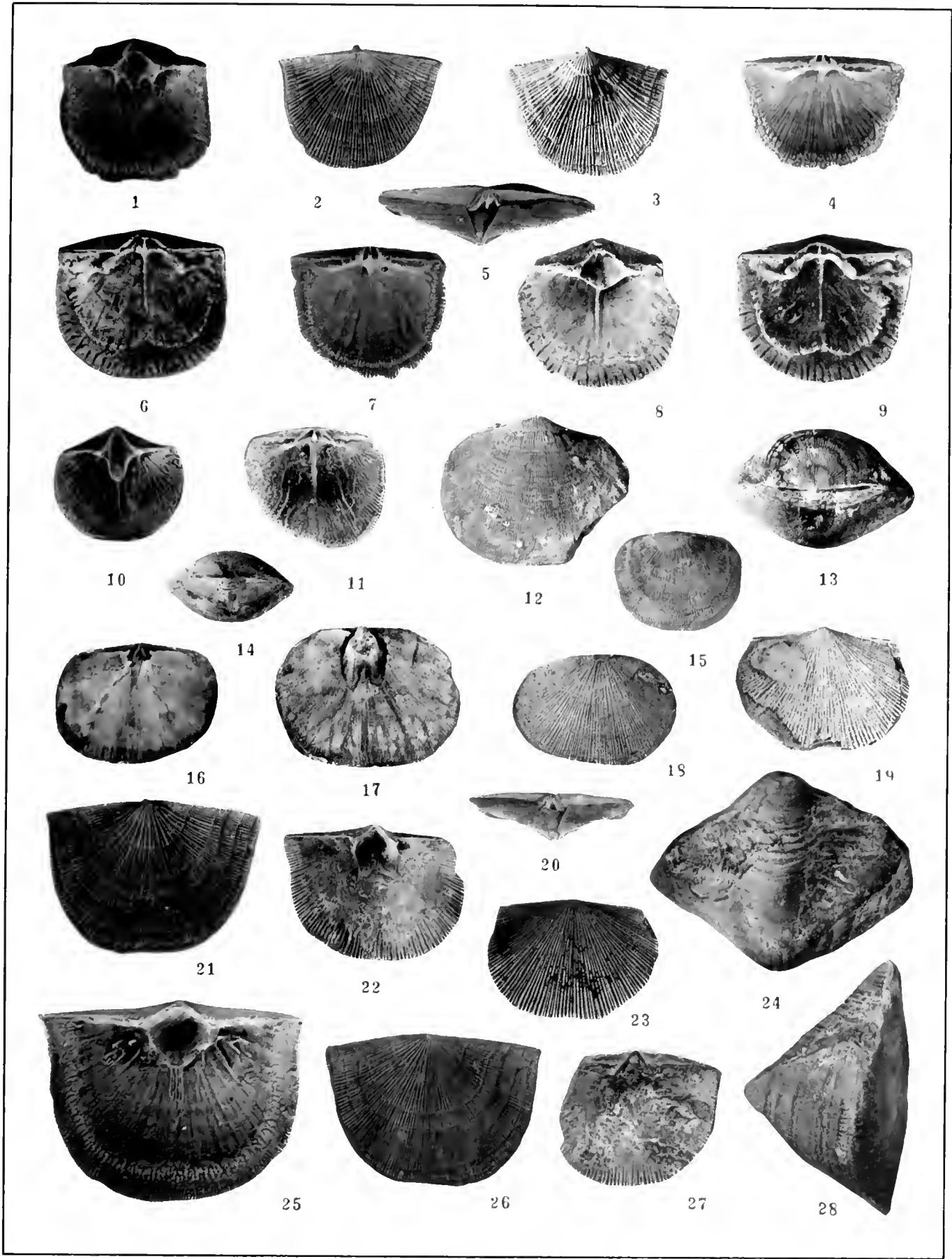


PLATE 9

FIGS. *Dinorthis sweeneyi* (Winchell)

- 1.—Ventral interior, showing form of muscle impressions and remnantal deltidium. x 1.5.
 - 10, 14.—Lateral and dorsal views of exterior, showing convexo-concave profile and costate exterior. x 1.5.
 - 11.—Dorsal interior, showing orthoid brachiophores and crenulated myophore of cardinal process. In its later stages of growth, the cardinal process may become distinctly lobate, see figs. 3 and 20. x 2.
- Ordovician (Decorah), St. Paul, Minn. Cat. Nos. S 686 and S 693.

Dinorthis pectinella (Emmons)

- 2.—Ventral interior of a silicified specimen, showing interior. x 1.
 - 5.—Exterior, x 0.75, with its costæ.
- Ordovician (Trenton), Curdsville, Ky. Cat. No. S 685.

Dinorthis (Plæsiomys) subquadrata (Hall)

- 3.—Dorsal interior, showing cardinal process of an old shell and lobation developed in late stages. x 2.
 - 20.—Same, x 3, showing myophore and shaft, also orthoid nature of brachiophores and swollen notothyrial platform. Cf. pl. 10, fig. 25.
- Ordovician (Richmond), Richmond, Ind. Cat. No. S 728.

Dinorthis (Pionorthis) sola (Billings)

- 4, 6, 7, 8.—Ventral, lateral, posterior, and dorsal views of a large specimen, showing ornamentation and lenticular outline of the species.
- Ordovician (Richmond), Pt. Carleton, Anticosti. Cat. No. S 760. x 1.5.
- 9.—Ventral internal mold, showing characteristic dinorthid muscle-scars.
- Ordovician, cliff, W. side Vauréal Bay, Anticosti. Cat. No. S 758. x 2.

Aff. *Dinorthis (Pionorthis) carletona* Twenhofel

- 13.—Ventral internal mold, showing muscle impressions.
- Ordovician, Raven Nest, Anticosti. Cat. No. S 754. x 1.5.

FIGS. *Dinorthis (Retrorsirostra) carleyi* (Hall)

- 21, 23.—Ventral and dorsal exteriors, showing procline ventral interarea.
- Ordovician (Arnheim), Jefferson Co., Ind. Cat. No. S 747. x 1.5.

Dinorthis (Retrorsirostra) carleyi insolens Foerste

- 22.—Ventral interior, showing teeth, crural fossetts, curving dental plates, and muscle impressions. Note absence of pallial marks.
- Ordovician (Waynesville)?, Hanover, Ohio. Cat. No. S 750. x 1.5.

Austinella sp.

- 12.—Ventral interior, showing large teeth and outline of muscle area.
- Ordovician (Maquoketa), Spring Valley, Minn. Cat. No. S 375. x 1.5.

Austinella whitfieldi (N. H. Winchell)

- 15.—Ventral internal mold, showing muscle-scars. These and the pallial trunks diverging from the anterior ends of the diductor impressions appear to relate the genus most closely to *Dinorthis*.
 - 16, 19.—Ventral and dorsal exteriors.
 - 18.—Reverse side of fig. 15, dorsal internal mold, showing adductor impressions.
- This genus has been referred to as a subgenus of *Plectorthis*, but structurally it has nothing to do with *Plectorthis* or the *Plectorthidæ*.
- Ordovician (Maquoketa), Spring Valley, Minn. Cat. Nos. S 374 and S 376 (figs. 16, 19). x 1.5.

Austinella scovillei (Miller)

- 22.—Ventral interior, showing teeth, crural fossettes, curv-
tinctly dinorthid in structure.
- Ordovician (Richmond), near Lebanon, Ohio. Cat. No. S 377. x 1.5.

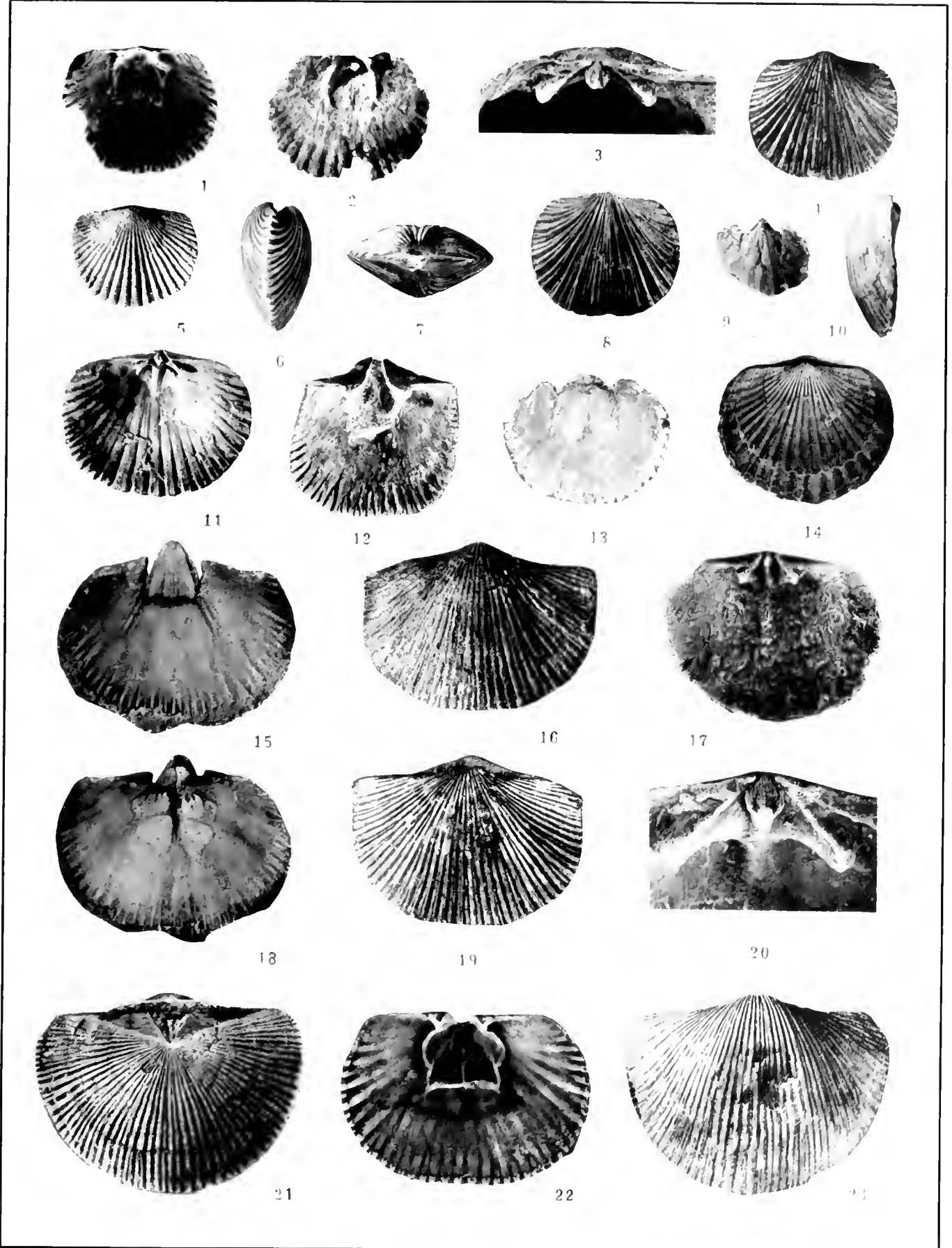


PLATE 10

FIGS. *Cyclocœlia sordida* (Hall)

- 1, 5.—Ventral and dorsal exteriors.
 2, 4.—Ventral and dorsal internal molds, the former showing short dental plates and the latter the mold of the median septum.
 Ordovician (Maysville, Fairmount), Cincinnati, Ohio. Cat. No. S 383. x 2.

Cyclocœlia sectistriata (Ulrich)

- 3, 7, 9.—Lateral, dorsal, and ventral views of exterior.
 Ordovician (Maysville, Fairmount), Cincinnati, Ohio. Cat. No. S 387 (one of Ulrich's type lot). x 2.

Skenidioides billingsi Schuchert and Cooper

- 6, 11, 13, 14.—Lateral, ventral, posterior, and dorsal views of holotype.
 8, 10, 12.—Dorsal interiors of paratypes, illustrating well high dorsal septum, cardinal process, and cruralium. Fulcral plates visible forming sockets. Brachiophores broken off, but when preserved, very long.
 Ordovician (Black River), Paquette Rapids, Ottawa River, Quebec. Cat. No. S 2013 (holotype, 2013a). x 4.

Dinorthis (*Plæsiomys*) *subquadrata* (Hall)

- 15.—Ventral internal mold, showing characteristic muscle-scars. The adjustor scars are prominent in the whole dinorthid stock.
 Ordovician (Richmond), Spring Valley, Minn. Cat. No. S 732. x 1.5.
 17, 18.—Dorsal and ventral exteriors. x 1.
 24.—Ventral interior, showing musculature and course of pallial markings. x 1.5.
 Ordovician (Richmond), Richmond, Ind. Cat. No. S 728.

FIGS. *Dinorthis* (*Plæsiomys*) *subquadrata* (Hall)—*Cont.*

- 25.—Dorsal interior, showing cardinalia. x 1.5.
 26.—Interior of a gerontic ventral valve, showing extreme thickening of shell. x 1.5.
 Ordovician (Richmond), Richmond, Ind. Cat. No. S 728.

Valcourea magna Schuchert and Cooper, n. sp.

- 16, 20, 27, 29.—Posterior, lateral, dorsal, and ventral views of exterior.
 28.—Ventral interior, showing musculature and pallial markings. This specimen is not provided with a deltidium but the pedicle callist is visible.
 Ordovician (Simpson). Criner Hills, Okla., sect. 35, 6 S, 1 E. Cotypes. Cat. No. S 779. x 1.5.

Valcourea deflecta (Conrad)

- 19.—Ventral interior, showing muscle-scars and deltidium in place.
 21.—Dorsal interior, showing cardinalia. Notothyrial platform greatly thickened.
 23.—Interarea of specimen shown in fig. 19, showing deltidium, and teeth with accessory sockets.
 Ordovician (Black River), Allen Hunter quarry, Fountain, Minn. Cat. No. S 771. x 1.5.

Valcourea loricula (Hall and Clarke)

- 22.—Ventral interior, showing musculature and lateral ovarian impressions. This specimen is not provided with a deltidium but in its place is a decided callist. This suggests that the deltidium, when present in *Valcourea* at least, is the seat of pedicle attachment.
 Ordovician (Black River), Allen Hunter quarry, Fountain, Minn. Cat. No. S 771a. x 1.5.

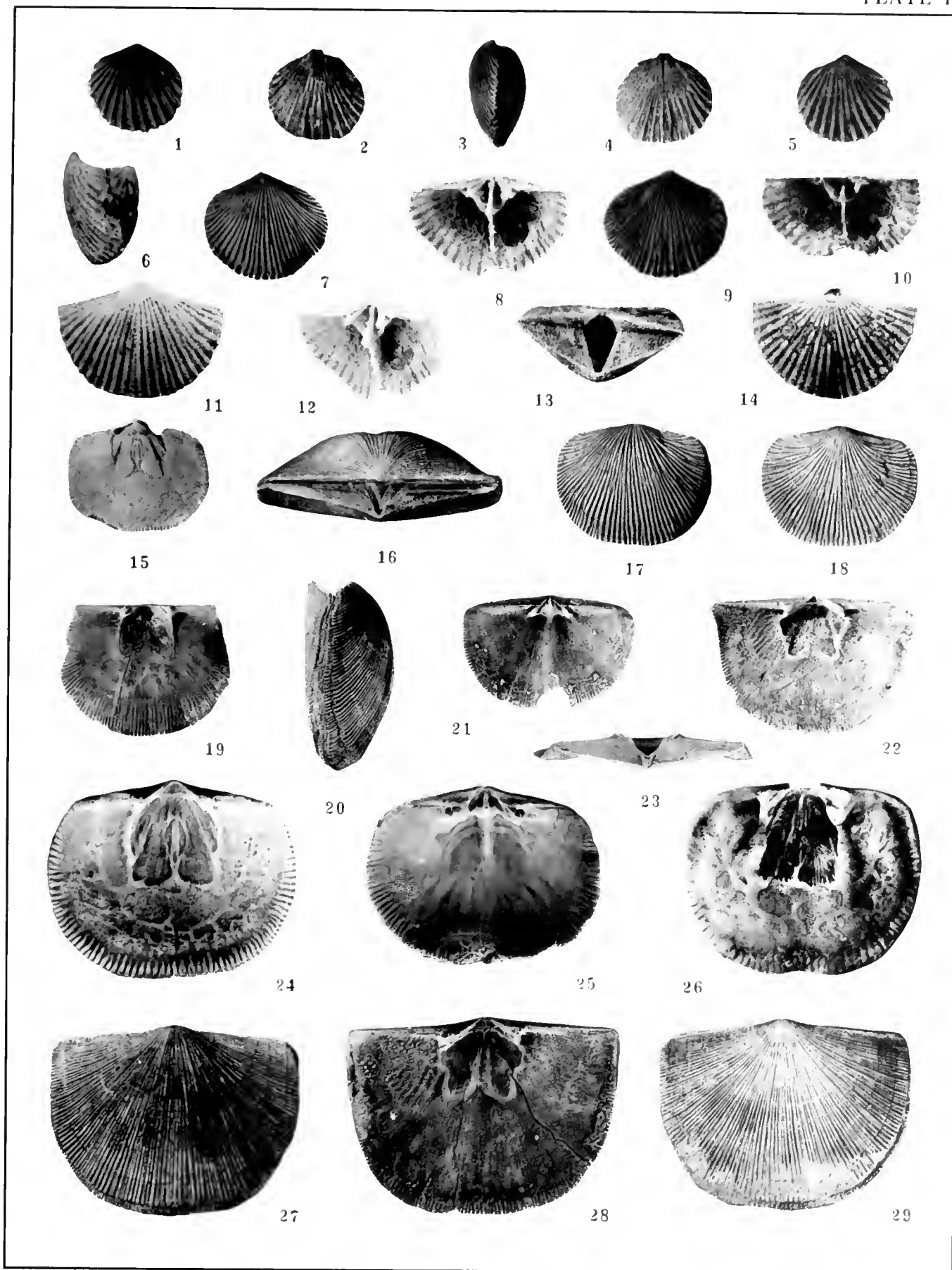


PLATE 11

Plectorthis fissicosta (Hall)

1, 3, 5, 15.—Dorsal, lateral, ventral, and posterior views of exterior.

Ordovician (Maysville), Cincinnati, Ohio. Cat. No. S 306. x 1.5.

Plectorthis jamesi (Hall)

2.—Ventral interior, showing dental plates and musculature. Cf. fig. 14.

Ordovician (Corryville), Cincinnati, Ohio. Cat. No. S 316. x 1.5.

Plectorthis plicatella (Hall)

4.—Dorsal interior. The incurving brachiophore plates which unite with the valve under the cardinal process are clearly visible. Cardinal process like that of *Hebertella*, see fig. 23.

9.—Ventral interior, showing a delicate dental plate.

Ordovician (Maysville), Cincinnati, Ohio. Cat. No. S 298. x 1.5.

Doleroides gibbosus (Billings)

6.—Ventral interior, to show characteristic musculature. Cf. fig. 24.

Ordovician (Decorah sh.), Minn. Cat. No. S 537. x 1.5.

16, 18.—Dorsal and ventral views of an old individual, showing normal wide sulcus.

Ordovician (Black River), Fountain, Minn. Cat. No. S 508. x 1.5.

Doleroides cf. gibbosus (Billings)

7, 8, 11.—Dorsal, ventral, and posterior views of exterior of a well preserved individual, showing pionodemoid outline. This particular specimen has a narrower fold and sulcus than is usual in the species.

Ordovician (Black River), Chatfield, Minn. Cat. No. S 507. x 1.5.

Doleroides pervetus (Conrad)

10, 13.—Dorsal and ventral views of exterior.

Ordovician (Black River), Lanesboro, Minn. Cat. No. S 498. x 1.5.

FIGS. *Doleroides pervetus* (Conrad)—Cont.

12.—Dorsal interior, showing cardinalia. Brachiophores supported by convergent plates as in *Plectorthis* and *Hebertella*.

Ordovician (Black River), Fountain, Minn. Cat. No. S 499. x 2.

Hebertella occidentalis sinuata (Hall)

14.—Young individual. Note resemblance to *Plectorthis*, figs. 2 and 9. x 2.

17, 23.—Enlarged views, x 1.75, of cardinalia of an old shell, showing shaft and compressed myophore of cardinal process, brachiophores and their supporting plates.

19, 20, 22, 25.—Lateral, ventral, dorsal, and posterior views of a large individual. Note convexo-concave profile. x 1.5.

24.—Ventral interior, showing muscle area with its double-track adductor impression and subcrescentic diductor scars. Adjustor impressions borne, when visible, on base of dental plates. Notice callus deposit at back end near pedicle callist; in some specimens this almost completely obliterates the posterior portion of the muscular field. x 2.

26.—Adult dorsal interior, showing cardinalia. Shaft of cardinal process simple, with compressed myophore. Brachiophores supported by converging plates which unite under the cardinal process; sockets defined by fulcral plates. This is different from the usual type in the Orthidæ, in which the brachiophores are simple rods or blades supported only by a swelling of adventitious shell. x 2.

Ordovician (Maysville), Cincinnati, Ohio. Cat. Nos. S 388 (figs. 19, 20, 22, 25), S 397 (figs. 14, 24), and S 451 (figs. 17, 23, 26).

Hebertella frankfortensis Foerste

21.—Ventral interior, showing bipartite adductor track. Cf. fig. 24.

Ordovician (Trenton), Frankfort, Ky. Cat. No. S 440. x 2.

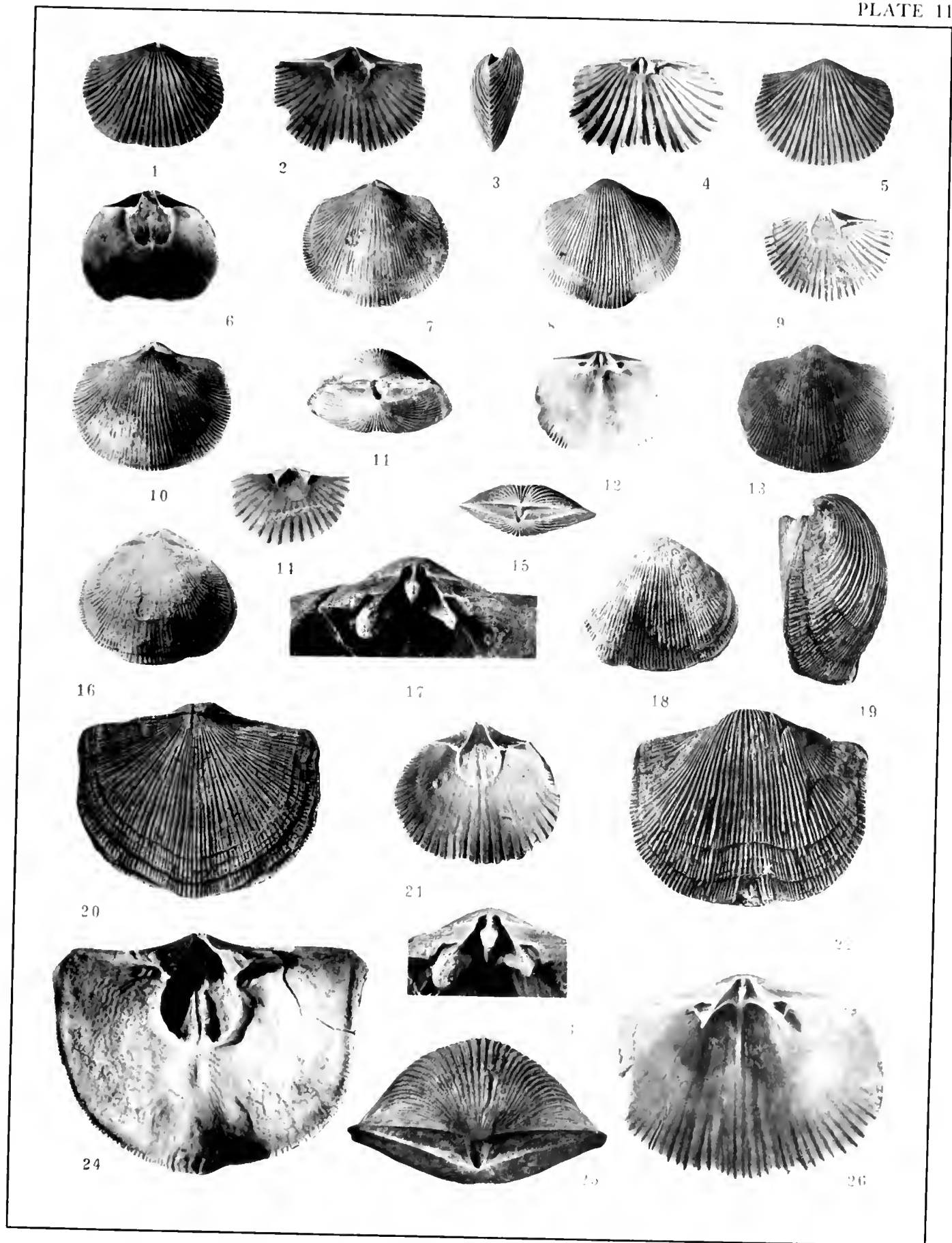


PLATE 12

FIGS. *Schizophorella fallax* (Salter)

- 1, 9.—Ventral interiors, the former an internal mold, x 2, and the latter an impression taken from it, x 1.5. Cat. No. B 52133, Brit. Mus. Nat. Hist.
- 2.—Dorsal exterior, x 1.5, the external mold corresponding to fig. 4. Cat. No. B 52123, Brit. Mus. Nat. Hist.
- 3.—Ventral exterior, x 1.5. Cat. No. B 52121, Brit. Mus. Nat. Hist.
- 4.—Dorsal internal mold, x 2. Cat. No. B 44610, Brit. Mus. Nat. Hist.
- 7.—Impression from the above, x 1.5, showing supporting plates of brachiophores.
Ordovician (upper Bala, Drummock group, Starfish bed), Thraive Glen, Girvan, Ayrshire, Scotland. Cat. Nos. S 486 and S 487. Impressions of British specimens.

Mimella globosa (Willard)

- 5, 10, 14, 15.—Posterior, dorsal, lateral, and ventral views of exterior. This species was previously referred to *Pionodema*, with which it forms a heterochronous homœomorph.
Ordovician (Chazy), Luttrell, Tenn. Cat. No. S 483. x 1.5.
- 6.—Dorsal interior, showing septum, cardinal process, and sessile cruralium.
- 8.—Ventral interior, showing trilobed muscle area.
Ordovician (Chazy), Washburn, Tenn. Cat. No. S 482. x 1.5.

Mimella melonica (Willard)

- 20.—Ventral interior, showing trilobed muscle field and pallial markings.
Ordovician (Chazy), Luttrell, Tenn. Cat. No. S 474. x 1.5.

Mcewanella lineolata (Savage)

- 11, 12.—Ventral valve, the latter showing the interarea.
- 18, 22.—Dorsal exterior and interior. Brachiophores of dorsal interior like those of *Platystrophia*, and the plates supporting them unite beneath the cardinal process.
- 21.—Ventral interior. Muscle-scars not defined and muscle field with thickened peripheral rim.
Ordovician (Fernvale), old quarry S. of Regenhart's quarry, N. W. edge of Cape Girardeau, Missouri. Cat. No. 65872, U. S. Nat. Mus. x 1.

FIGS. *Mcewanella raymondi* Foerste

- 17.—Ventral exterior, to show characteristic ornamentation. Ordovician (top of Kimmswick), Cape Girardeau, Missouri. U. S. Nat. Mus. x 1.5.

Platystrophia crassa (James)

- 13.—Dorsal interior, showing gerontic condition of cardinalia.
Ordovician (Maysville), Spring Valley, Minn. Cat. No. S 583. x 1.5.

Platystrophia laticosta (Meek)

- 16.—Dorsal interior, showing incurving brachiophore plates which are clearly visible only in young *Platystrophia*. Cf. *Plectorthis*, pl. 11, fig. 4.
- 23.—Ventral interior of young shell, showing dental plates and muscle area. Dental plates not visible in gerontic shells, see fig. 26.
- 27.—Dorsal interior, showing muscle impressions and cardinalia. The cardinal process of *Platystrophia* is usually much aborted. This figure shows the brachiophores and their supporting plates much thickened by callus deposit.
Ordovician (Maysville), Cincinnati, Ohio. Cat. No. S 575. x 1.5.

Platystrophia cf. laticosta (Meek)

- 19.—Very young dorsal valve, showing strongly incurving brachiophore plates and fulcral plates. Cf. similar views of *Plectorthis* and *Hebertella*.
Ordovician (Maysville), Roh's Hill, Cincinnati, Ohio. Cat. No. S 566. x 3.

Platystrophia acutilirata (Conrad)

- 24.—Ventral interior of gerontic individual. Dental plates obsolete and interior pitted by ovarian? impressions.
Ordovician (Whitewater), Oxford, Ohio. Cat. No. S 545. x 1.5.

Platystrophia ponderosa Foerste

- 25.—Dorsal interior, showing a gerontic individual. Cardinalia so thickened as to obliterate fulcral plates and exaggerate brachiophore supports. x 1.5.
- 26.—Gerontic ventral valve. Dental plates obsolete, owing to filling in of umbonal cavities. x 1.
Ordovician (Maysville), Cincinnati, Ohio. Cat. No. S 556.

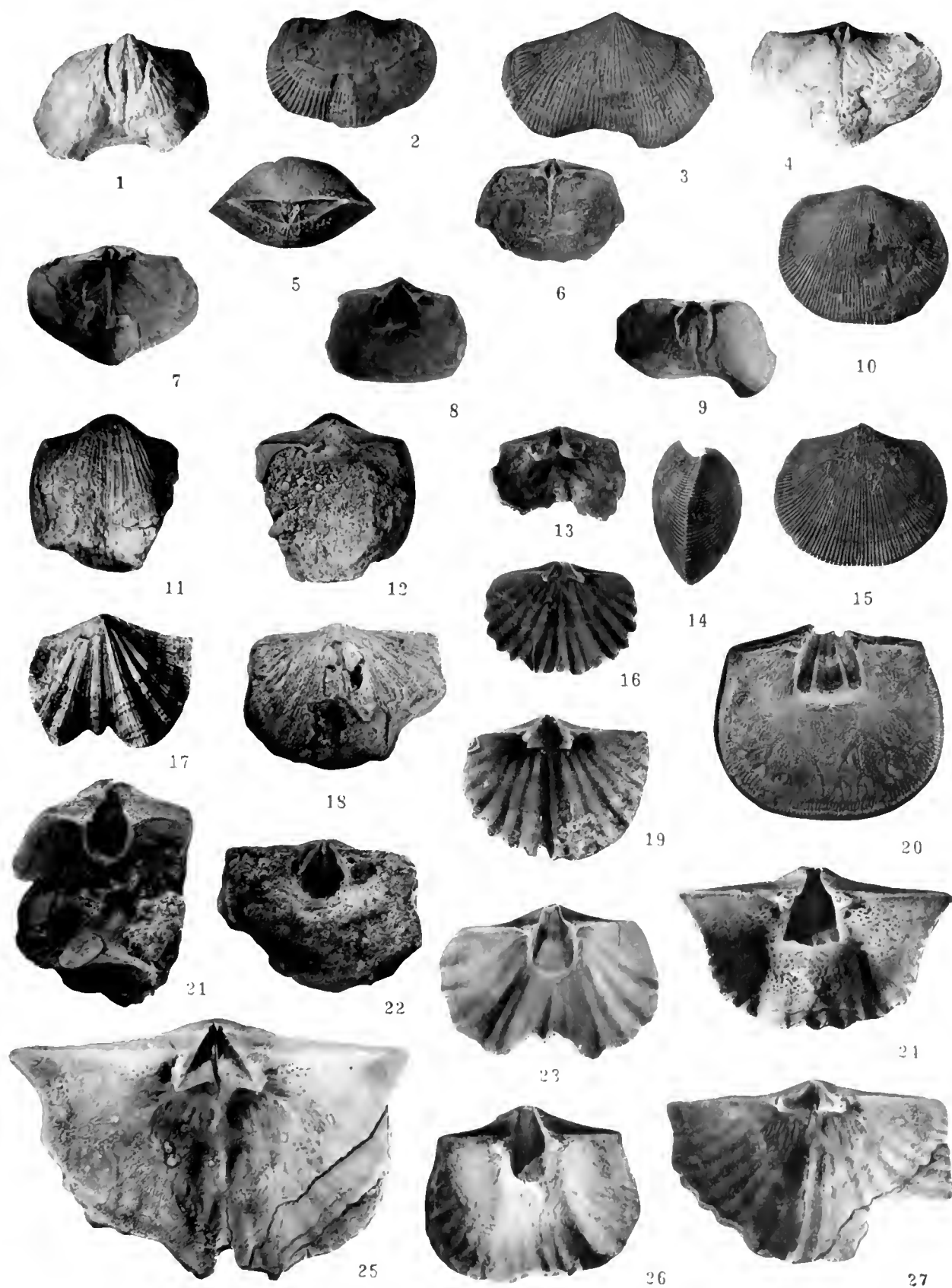


PLATE 13

FIGS. *Skenidium insigne* (Hall)

- 1, 2, 5, 8.—Posterior, anterior, dorsal, and postero-dorsal views of three individuals, showing characteristic external form. Figs. 1 and 8 show uncovered delthyrium, and spondylium.
 3.—Dorsal interior, showing wide hinge-plate.
 4.—Ventral interior, showing spondylium.
 Devonian (New Scotland), Indian Ladder, Albany Co., N. Y. Cat. No. S 2025. x 6.

Finkelburgia sp.

- 6, 11.—Ventral exterior, and interior showing pseudospondylium.
 Ozarkian (Eminence, near top), S. slope of hill $4\frac{3}{4}$ to 5 miles S. of Potosi, Missouri. Wax impressions from originals in U. S. Nat. Mus. Cat. No. S 60. x 3.

Finkelburgia sp.

- 7, 18.—Dorsal interiors, showing incurving brachiophore plates and subradial muscle impressions and strongly elevated ridges about each impression.
 Ozarkian (Huzzah Creek section, bed 7), 10 miles E. of Slideville, Missouri. Wax impressions from originals in U. S. Nat. Mus. Cat. No. S 58. x 3.

Finkelburgia armanda (Billings)

- 9, 10.—Dorsal internal mold, and wax impression taken from it.
 12.—Wax impression of ventral exterior, showing sculpture.
 15.—Wax impression of dorsal interior. This and fig. 10 show the simple cardinal process and the incurving brachiophore plates, and the fulcral plates. Structure much like that of *Hebertella* or *Plectorthis*.
 Ozarkian (near base of Logan's B₃) near Phillipsburg, Quebec. Cat. No. S 2109. x 2.20.

FIGS. *Finkelburgia* sp.

- 13, 17.—Dorsal and ventral exteriors of a silicified specimen.
 16.—Dorsal interior, reverse of fig. 13, showing converging brachiophore plates and elevated seats of muscle attachment.
 19.—Ventral interior, reverse of fig. 17, showing pseudospondylium.
 Ordovician (Canadian), 3 miles S. E. of Rainy Mt., Kiowa Co., Okla. Ulrich Coll., U. S. Nat. Mus. x 3.

Finkelburgia aff. *osceola* (Walcott)

- 14.—Ventral internal mold, showing filling of delthyrial cavity.
Finkelburgia appears to be the earliest genus in the plectorthid line.
 Ozarkian, Crawford Co., Missouri. Cat. No. S 62. x 3.

Angusticardinia recta (Pander)

- 20, 22.—Ventral and dorsal views of this rhynchonelloid orthid.
 21.—Dorsal interior, showing brachiophores and their supporting plates which unite at the floor of the valve with the median ridge, forming a narrow notothyrial orthid.
 Ordovician (Walchow, Glauconite ss., B_{1β}), Popovka, near Leningrad, Russia. Cat. No. S 171. x 3.

Angusticardinia striata (Pander)

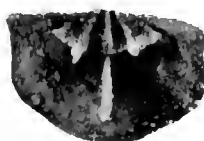
- 23.—View showing profile.
 Ordovician (Walchow, Glauconite ss., B_{1β}), Popovka, near Leningrad, Russia. Cat. No. S 170. x 3.



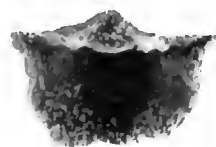
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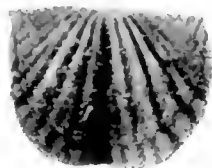
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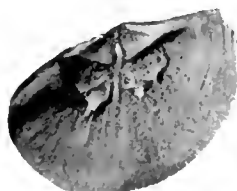
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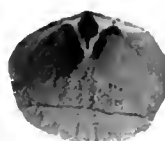
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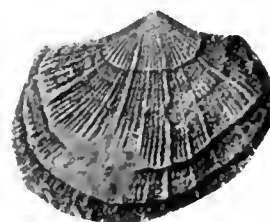
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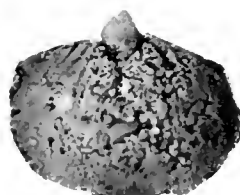
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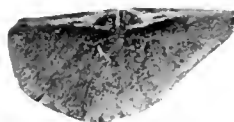
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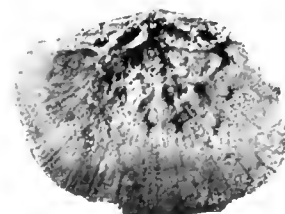
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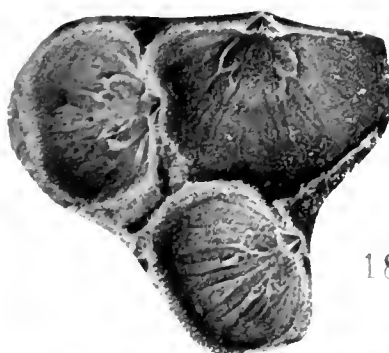
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23

PLATE 14

FIGS. *Porambonites teretior* (Eichwald)

- 1, 2, 4, 5, 10.—Dorsal, anterior, posterior, ventral, and lateral views of a rather smooth, attenuate type.
Ordovician (Mohawkian, Kuckers), near Jewe, Estonia. Cat. No. S 1520. x 1.

Porambonites deformatus (Eichwald)

- 6, 7, 9.—Posterior, ventral, and lateral views of a coarsely pitted, attenuate type.
Ordovician (Mohawkian, Echinosphærites ls.). Popovka, near Leningrad, Russia. Cat. No. S 1528. x 1.5.

Porambonites baueri Noetting

- 8.—Dorsal interior, showing great internal thickening of brachiophore (spondyloid) plates.
24.—Dorsal interior of a gerontic individual, showing greatly thickened brachiophore plates.
Ordovician (Mohawkian, Jewe, D₁), near Jewe, Estonia. Cat. No. S 1529. x 1.

Porambonites gigas Schmidt

- 14.—Posterior view, showing resorbed beaks. This condition of the beaks indicates that the pedicle persisted throughout the life of the animal.
Ordovician (Richmond, Lyckholm, F₁), Kurkül, Estonia. Cat. No. S 1518. x 0.5.

Porambonites reticulatus Pander

- 3, 11-13.—Posterior, dorsal, ventral, and lateral views of the same individual, showing suborbicular outline and characteristic ornamentation.
15.—Anterior view of another individual, showing deep ventral sulcus and long tongue.
Ordovician (Chazy, Walchow), Iswos on Walchow River, Russia. Cat. No. S 1532. x 1.

FIGS. *Porambonites reticulatus* Pander—*Cont.*

- 29.—Enlargement of a portion of fig. 11, to show ornamentation in greater detail.
Ordovician (Chazy, Walchow), Iswos on Walchow River, Russia. Cat. No. S 1532.

Porambonites schmidtii Noetting

- 20, 27.—Views of ventral interior, the former tipped forward to show better the dental plates. These plates are discrete but in old forms may unite by secondary deposition on their sides and the floor of the valve.
21, 28.—Two views of a dorsal valve belonging to the ventral one above. In fig. 28, the reader is looking directly into the shell and the short brachiophore plates are not visible but the sockets are clearly discernible. In fig. 21, the front of the shell is tipped forward to permit a view of the brachiophore plates, which are also discrete. There are no structures in either of these two shells or in the genus linking them to the Pentameridæ.
Ordovician (Mohawkian, Jewe, D₁), Spitham, Estonia. Cat. No. S 1530. x 1.

Lycophoria nucella (Dalman)

- 16, 18.—Ventral interiors, showing discrete dental plates.
22, 23.—Dorsal interiors, showing cardinal process.
30.—Same as fig. 22, enlarged three times to show greater detail. Cardinal process complete and uninjured in any way, not forked as Hall and Clarke assert. Compressed brachiophore plates visible, and also short brachiophores.
Ordovician (Chazy, Kunda). Popovka, near Leningrad, Russia. Cat. No. S 1515. x 1.5 (except fig. 30).
17, 19, 25, 26.—Lateral, ventral, dorsal, and posterior views of a complete individual, showing contour, profile, and ornamentation.
Ordovician (Chazy, Kunda, B₃), Popovka, near Leningrad, Russia. Cat. No. S 1516. x 1.5.

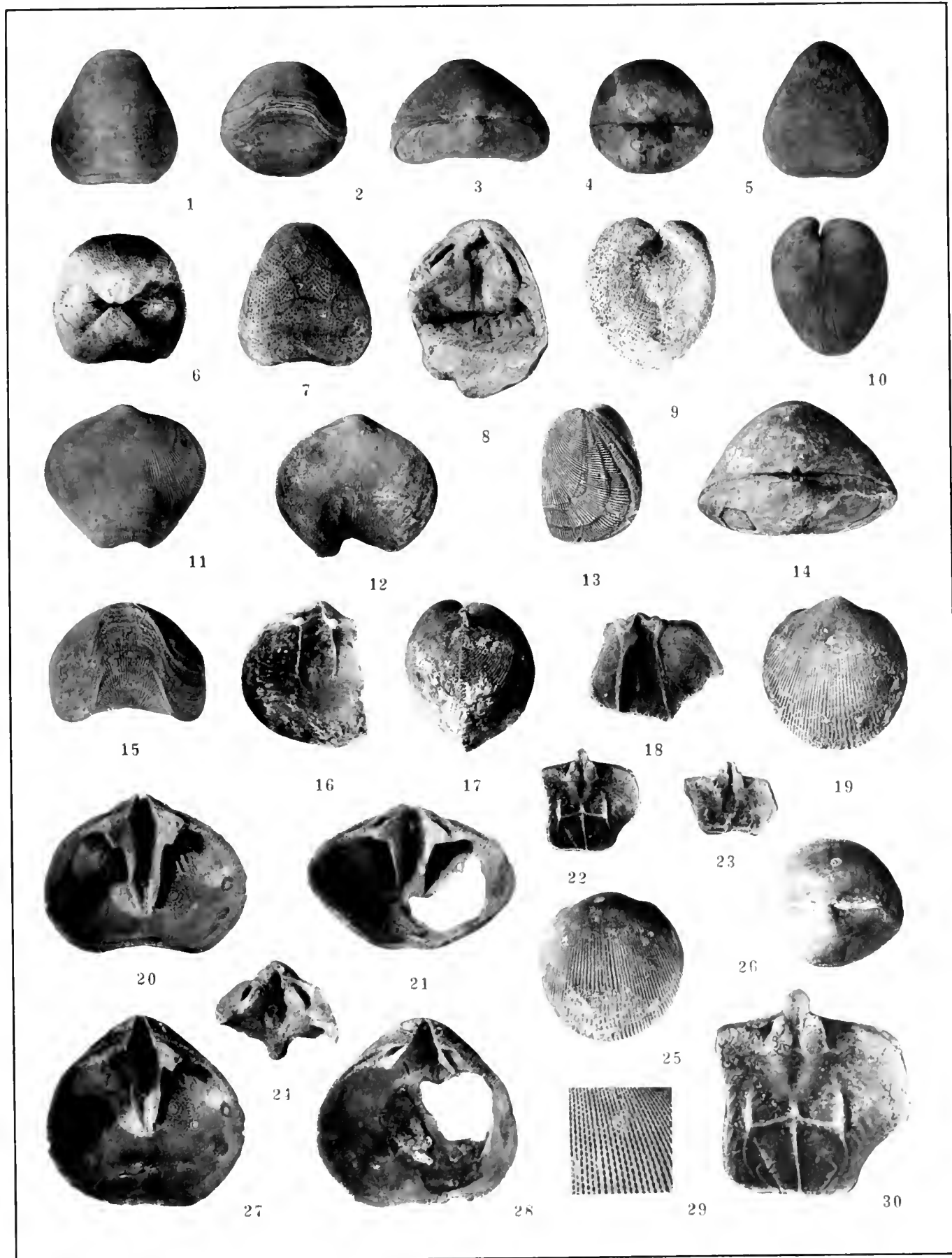


PLATE 15

FIGS. *Syntrophina campbelli* (Walcott)

- 1.—Ventral internal mold, showing impression of spondylium.
 2, 19.—Dorsal interiors, showing subparallel or divergent brachiophore plates. Fig. 19 also shows impression of small callosity at back of notothyrial cavity.
 Ordovician (Canadian, lower Roubidoux), hill opposite McCabe, Missouri. Cat. No. S 1553. x 2.65.

Syntrophina brevisseptata Ulrich MS.

- 15, 16.—Ventral interiors, 15 being an internal mold and 16 an impression taken from it. Spondylium well shown.
 17, 18.—Dorsal interiors, the latter an internal mold and the former an impression taken from it, showing divergent brachiophore plates.
 Ozarkian?, Phillipsburg, Quebec. Cat. No. S 1551. x 2.

Syntrophina palmata (Cleland)

- 30, 31.—Dorsal internal mold and impression taken from it. The latter shows the adductor impressions and the posterior callosity.
 Ordovician (Canadian, Tribes Hill), Fort Hunter, N. Y. Cat. No. S 1544. x 2.65.

Syntrophia cf. *lateralis* (Whitfield)

- 3.—Replica of dorsal interior, from original in Ulrich Coll., U. S. Nat. Mus. Shows narrow, short cruralium, which resembles that of some rhynchonelloids.
 Ozarkian? (B₃), Phillipsburg, Quebec. Cat. No. S 1574. x 2.

Syntrophia lateralis (Whitfield)

- 27, 28.—Lateral and front views of ventral interior, the latter showing musculature.
 29, 32.—Posterior and dorsal views of complete individual. From Walcott, Camb. Brach., pl. 102, figs. 6e-g, after Hall and Clarke, Pal. N. Y., vol. 8, pt. 2, pl. 62, fig. 9.

Syntrophinella typica Ulrich MS.

- 4, 5.—Ventral and dorsal exteriors, showing faint radial sculpture.
 13.—Dorsal interior.
 Ozarkian? (upper Chepultepec), ½ mile S. W. of Elliottsville church, Bess quad., Alabama. Wax replicas of originals in Ulrich Coll., U. S. Nat. Mus. Cat. No. S 1582. x 2.65.

FIGS. *Syntrophoides harlanensis* (Walcott)

- 20.—Ventral interior, with pseudospondylium and divergent pallial markings.
 23.—Dorsal interior, with adductor impressions and anterior pallial markings.
 Up. Cambrian, 4 miles N. E. of Rogersville, Tenn. Replicas of Walcott's types (Cat. No. 52252, U. S. Nat. Mus.). Cat. No. S 1583. x 2.

Clarkella sp.

- 6, 11.—Ventral interiors, showing spondylium.
 7, 10.—Dorsal interiors, showing numerous septa supporting brachiophore plates. These are not continuous across the middle of the valve but separate as in *Syntrophina*.
 Ozarkian?, Phillipsburg, Quebec. Cat. No. S 1567. x 3.

Clarkella aff. *C. montanensis* (Walcott)

- 8, 9.—Ventral and dorsal exteriors, showing smooth surface.
 Ozarkian? (Logan's B₁), near Phillipsburg, Quebec. Geol. Surv. Canada. x 2.

Multicostella platys (Billings)

- 12.—Lenticular profile.
 Ordovician (Chazy), Speer's Ferry, Va. Cat. No. S 792. x 2.

Huenellina triplicata (Walcott)

- 14, 21.—Ventral and dorsal internal molds. Ventral interior shows an impression of the pseudospondylium and radiating ridges diverging from it and a strong anterior adductor (?) impression. Fig. 21 shows molds of peculiar lateral plates upon which the genus is based. Original in U. S. Nat. Mus.
 22.—Replica of fig. 21, to show lateral plates.
 Ozarkian?, Novaya Zemlya, Russia. Cat. No. S 1580. x 2.65.

Yangtzeella poloi (Martelli)

- 24, 25.—Ventral and posterior views of exterior.
 Up. Ordovician, Foopé, China. Cat. No. S 1585. x 1.33.
 26.—Dorsal exterior.
 Ordovician (Neichiashan), Neichiashan, Yangtze gorge, Hupeh, China. Cat. No. S 1586. x 1.30.

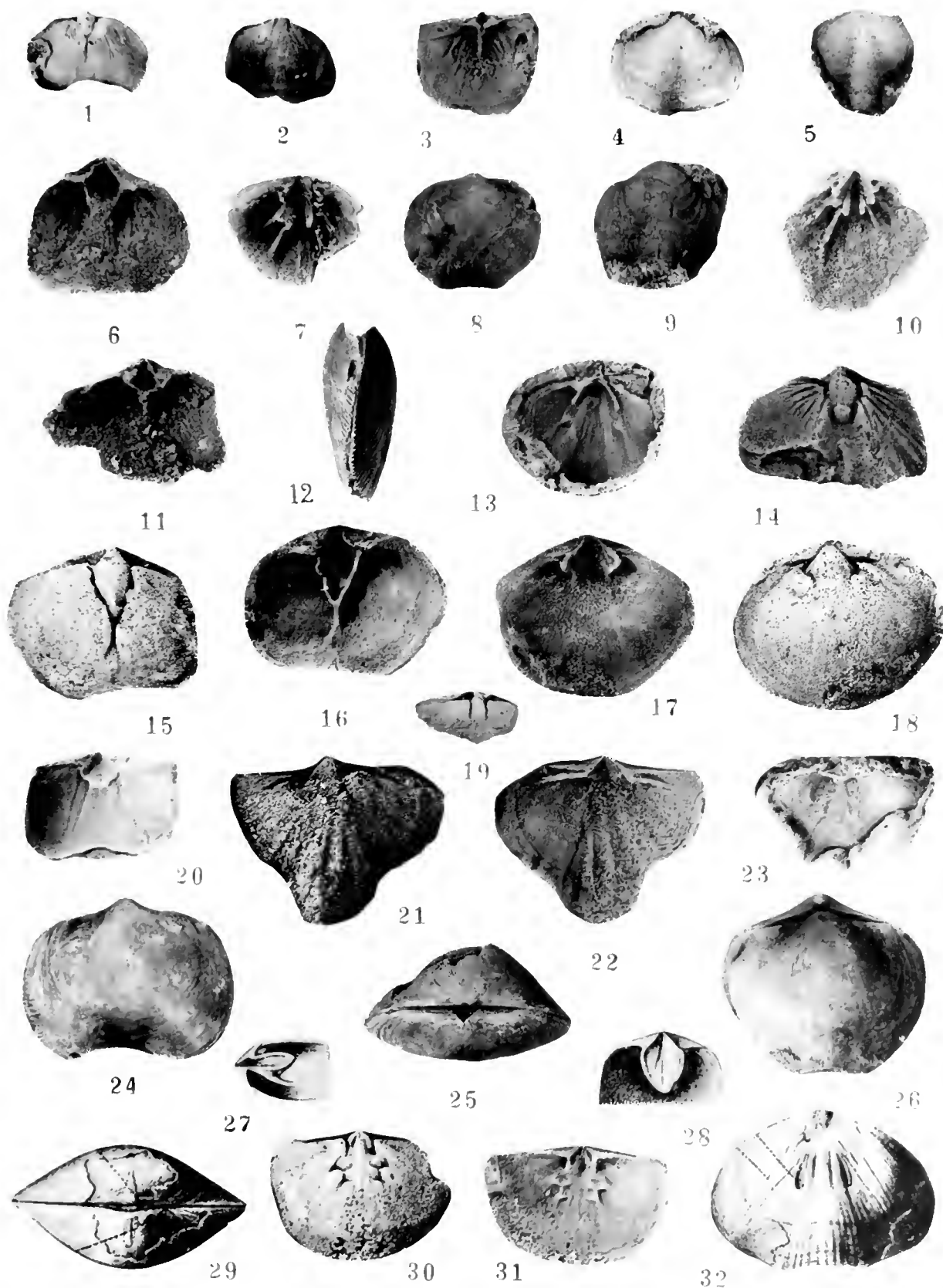


PLATE 16

FIGS. *Mystrophora areola* (Quenstedt)

- 1, 5.—Dorsal and ventral exteriors of a large specimen. Compare the ornamentation and contour with those of *Skenidium*, pl. 13.
2, 3, 4.—Dorsal, lateral, and ventral views of a smaller specimen.
Devonian (Givetian, crinoid bed), Gerolstein, Germany. Cat. No. S 2110. x 2.7.

Orthorhynchula ottawaensis (Billings)

- 6.—Ventral interior of a silicified specimen, showing long dental plates.
9, 13.—Crural bases with ends of crural processes, which are extremely long when present.
Certain rhynchonelliform shells from Kentucky have been referred to this species, but they should be placed with *Camerella*. The Ottawa forms (topotypes) have commonly been referred to *Camerella* but belong with *Orthorhynchula*. "*Camerella*" *panderi* from Paquette Rapids, an associate of *C. ottawaensis*, is neither a *Camerella* nor an *Orthorhynchula*, but allies itself with the spire-bearing genera.
Ordovician (Black River), Paquette Rapids, Ottawa, Canada. Cat. No. S 809. x 2.7.

Orthorhynchula linneyi (James)

- 12.—Silicified specimen from which the ventral valve has been broken, revealing the crural bases.
28, 29.—Dorsal and lateral exteriors.
Ordovician (Maysville), Frankfort, Ky. Cat. No. 7539 Y. P. M. x 2.
17.—Ventral view of exterior.
30.—Ventral interior, showing teeth, interarea, and outline of muscular field.
Ordovician (Maysville), Colby, Clarke Co., Ky. Cat. Nos. S 795 and S 796 (fig. 30). x 2.

Kayserella lepida (Schnur)

- 7, 8, 10.—Posterior, lateral, and ventral views of exterior. Posterior view shows deltidium indistinctly.
Devonian (Eifelian), Gerolstein, Germany. Cat. No. S 2111. x 2.

FIGS. *Taffia planoconvexa* Butts

- 11.—Dorsal interior, showing orthoid character of cardinalia.
Low. Ordovician (Odenville), E. of Odenville, Alabama. U. S. Nat. Mus.

Pomatotrema grandæva (Billings)

- 14, 19.—Dorsal and ventral exteriors.
16, 23, 26, 31.—Ventral interiors, showing deltidium, dental plates, internal lateral ovarian ridges, and a ridge developed from the adductor impression.
18, 21.—Dorsal interiors, showing lateral ridges and simple cardinal process. The specimen in fig. 21 was actually in conjunction with that in fig. 16.
Pomatotrema shows many resemblances to the Clitambonacea and, together with the members of the Clitambonitidæ, has been placed in that superfamily.
Ordovician (Beekmantown), Newfoundland. Cat. Nos. S 81 (fig. 18) and S 82. x 2.7.

Pomatotrema muralis Ulrich and Cooper, n. sp.

- 15.—Ventral interior.
20.—Dorsal internal mold. Compare these figures with those of *P. grandæva*.
Ordovician (upper Canadian), Ardmore quad., Okla. Wax impressions of specimens in U. S. Nat. Mus., Cat. Nos. S 77 (fig. 20) and S 79. x 2.7.

Planidorsa crassicostella Schuchert and Cooper, n. sp.

- 22, 27.—Posterior and ventral views of the holotype, the former showing chilidial plates.
Ordovician (Chazy), Speer's Ferry, Virginia. Cat. No. S 763. Fig. 22 x 1.35.

Planidorsa bella Schuchert and Cooper

- 24.—Dorsal exterior, x 1.35.
25.—Ventral internal mold, showing musculature, which is essentially dinorthoid but with unusually large adductor scars. x 2.
Ordovician (Chazy), Washburn, Tenn. Holotype. Cat. No. S. 764.

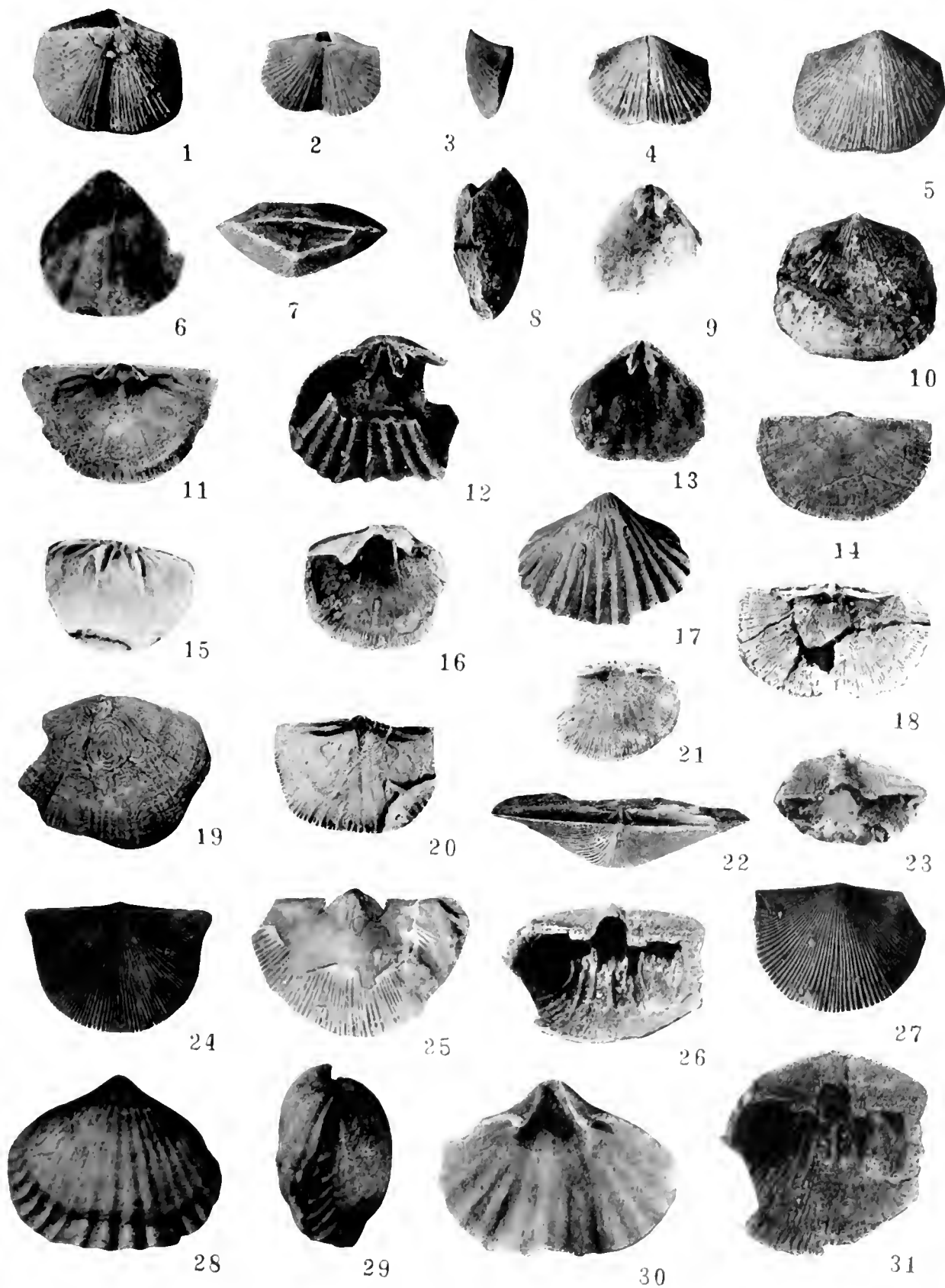


PLATE 17

FIGS. *Onniella bröggeri* Bancroft

- 1, 6.—Dorsal and ventral views, showing exterior.
Ordovician, Horderley District, E. Shropshire, England. Cat. No. S 2112. x 2.

Onniella sp.

- 8, 12.—Dorsal internal mold and impression taken from it.
9, 11.—Ventral internal mold and replica of it.
18.—Enlargement, x 4, of fig. 12, showing internal structure in greater detail. Cf. fig. 23.
Up. Ordovician, Horderley District, E. Shropshire, England. Cat. No. S 2113. All except fig. 18 x 2.

Dalmanella rogata (Sardeson)

- 2, 31.—Dorsal interior, x 2.65, and enlargement of same, x 4, showing simple, bladelike brachiophores and cardinal process. The myophore is lobed and from its center there has grown forward along the shaft a peculiar process giving the whole the appearance of the head of a bee.
Ordovician (Black River), St. Paul, Minn. Cat. No. S 845.
3, 5.—Ventral and dorsal exteriors, showing suborbicular outline and ornamentation.
4.—Ventral interior, showing characteristic bilobed muscle field.
Ordovician (Trenton), 3 miles S. E. of Cannon Falls, Minn. Cat. No. S 811. x 2.67.
7, 13.—Dorsal and ventral views of the exterior of Sardeson's holotype.
Ordovician (fucoid bed), Ellsworth, Wis. Cat. No. S 935. x 2.

Dalmanella meeki (Miller)

- 10, 20, 21.—Posterior, ventral, and dorsal exterior views, x 1.5. This transverse type of shell strongly resembles Bancroft's *Onniella*.
23, 24.—Dorsal interiors, showing age variations. Fig. 23 portrays the younger shell, with its more slender cardinal process having a lobed myophore, indistinct adductor impressions, and bladelike brachiophores with little adventitious thickening. The other shell shows a prominent thickening of the cardinal process, with some development of adventitious testaceous matter on the inside surface of the brachiophores, and the adductor impressions are more distinct. x 2.
33.—Ventral interior, showing well the dental plates and deep crural fossettes. Notice that the musculature varies from that usual in *Dalmanella rogata* and allies in not being lobate in front and in having the adductor track approximately the same length as the diductor impressions. The "meeki" type of *Dalmanella* may be referable to *Onniella* when that genus has become better established and its lineage put on a substantial basis. x 2.
Ordovician (Richmond), Hanover, Ohio. Cat. No. S 855.

FIGS. *Dalmanella ignota* (Sardeson)

- 19.—Internal mold, showing musculature. Adjustor scars and elongate diductor impressions visible enclosing adductor impressions. Such a muscle pattern could have produced that of *Rhipidomella* by expansion of the diductor impressions to a semiflabellate outline.
Ordovician (Wykoff), Spring Valley, Minn. Cat. No. S 947. x 2.

Dalmanella emacerata (Hall)

- 22.—Ventral internal mold showing bilobate muscle area and pallial markings. Cf. interior of *Parmorthis*, pl. 21.
Ordovician (Maquoketa), Granger, Minn. Cat. No. S 954. x 2.

Dalmanella corpulenta (Sardeson)

- 25.—Ventral internal mold, showing lobate muscle-scars. x 1.5.
27, 29.—Dorsal interior and exterior. x 2.
Ordovician (Richmond), Spring Valley, Minn. Cat. No. S 867.

Dalmanella tersa (Sardeson)

- 26, 30.—Dorsal interior, showing brachiophores, and dorsal exterior. This shell is plano-convex in profile and the ventral diductor scars wrap around the adductor impressions. *D. tersa* has all the characters necessary to produce *Rhipidomella*.
Ordovician (Richmond), Wilmington, Ill. Cat. No. S 871. x 2.

Resserella canalis (Sowerby)

- 14.—Ventral internal mold, showing divergent pallial marks.
15, 16.—Dorsal internal mold, and impression taken from it. Note, in the latter, structure identical with that of *D. rogata* (figs. 2, 31).
Ordovician (low. Longvillian, Kjærina zone), Long Lane quarries S. of Horderley, E. Shropshire, England. Cat. Nos. S 2114 (fig. 14) and S 2115. x 2.

Heterorthina præculta Bancroft

- 17.—Ventral internal mold, x 1.5, showing pallial markings.
28.—Ventral internal mold, showing musculature. x 1.5.
32.—Cardinalia of dorsal valve, x 4. Bilobed myophore and cleft shaft clearly visible, also simple bladelike brachiophore plates.
Ordovician (Marshbrookian, *Wattsella watsi* zone), Horderley District, E. Shropshire, England. Cat. No. S 2116.

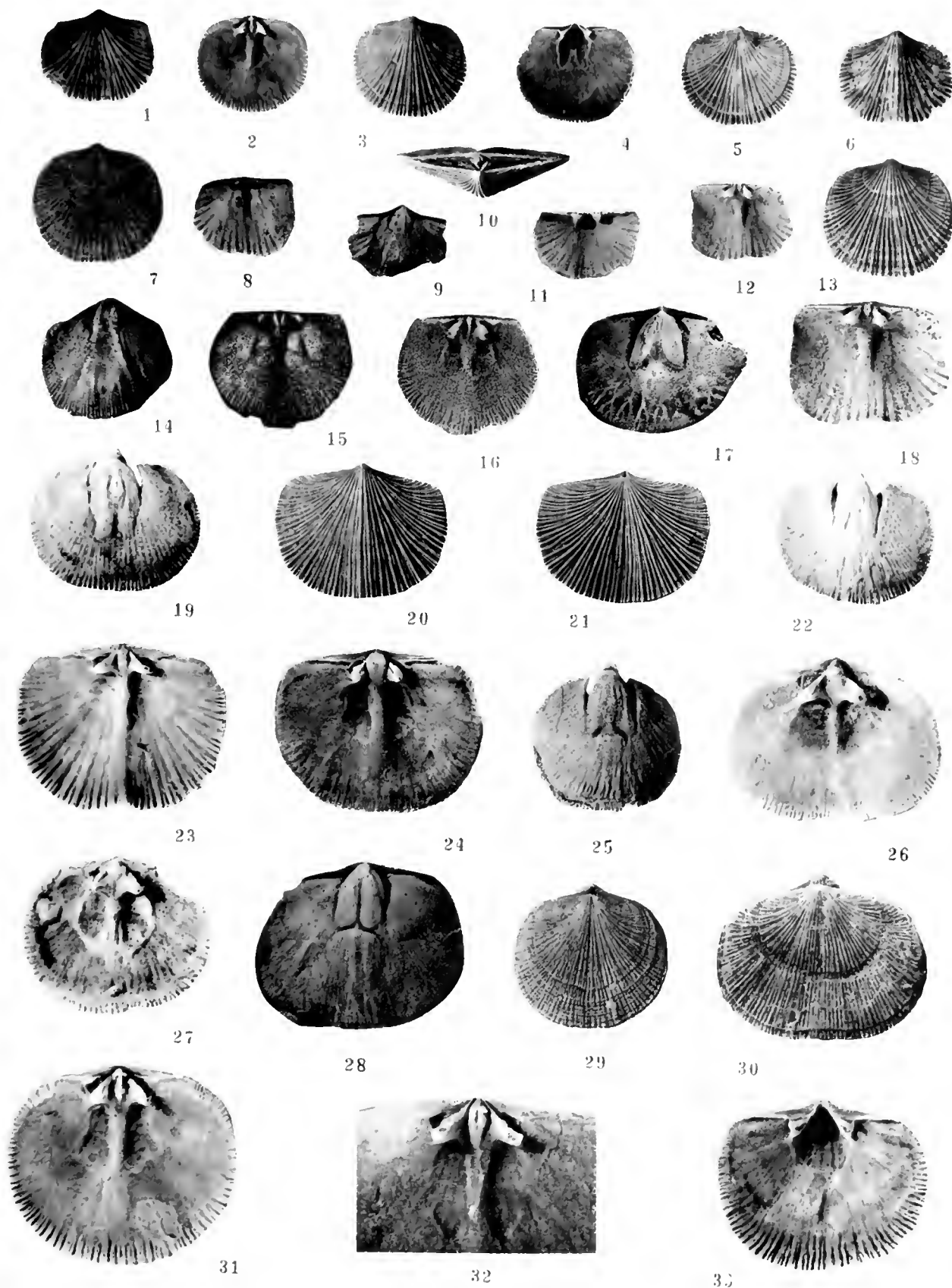


PLATE 18

FIGS. *Heterorthina fairmountensis* (Foerste)

- 1.—Ventral interior, showing widely divergent diductor impressions and delicate pallial markings. x 2. Cf. pl. 17, fig. 17.
- 2, 3.—Dorsal and ventral exteriors. x 1.5.
- 4.—Dorsal interior, to show cardinalia and musculature. Notice lobed myophore and cleft shaft of cardinal process, and simple divergent brachio-phores. Cf. fig. 7. x 2.
Ordovician (Bellevue), Hamilton, Ohio. Cat. No. S 852.

Heterorthina præculta Bancroft

- 5.—Ventral exterior, showing form of valve.
Ordovician (Marshbrookian), Horderley District, E. Shropshire, England. Cat. No. S 2117. x 1.5.
- 6, 7.—Internal mold of dorsal valve and wax replica made from it. Compare this replica with fig. 4; the former shows the same cleft shaft and lobate myophore, similar brachio-phores, muscle impressions, and pallial marks.
- 8.—Replica of a dorsal external mold. Dorsal valve flat and shell multicostellate.
Ordovician (Marshbrookian, *Wattsella watti* zone), Horderley District, E. Shropshire, England. Cat. No. S 2116. x 1.5.

Cariniferella carinata (Hall)

- 9.—Ventral internal mold, showing muscle field and form of muscle impressions.
- 15.—Dorsal internal mold, showing impressions left by brachio-phores and cardinal process.
- 16.—Wax impression taken from above.
Devonian (Chemung), Bath, N. Y. Cat. No. S 1087. x 1.5.
- 10, 12.—Ventral and dorsal exteriors, showing prominent dorsal sulcus and ventral fold.
Devonian (Chemung), Arkport, N. Y. Cat. No. S 1088. x 1.5.

Cariniferella dumonti (Verneuil)

- 11.—Ventral interior, showing musculature.
Up. Devonian, ? Belgium. Mus. Comp. Zool., Harvard Coll. x 1.5.

Linoporella punctata (Verneuil)

- 13, 14, 18.—Ventral interiors, showing respective stages in development of pseudospondylium. Fig. 18 shows discrete dental plates with little or no adventitious thickening on floor of delthyrial cavity. Fig. 14 shows an advanced stage in which the deposit is elevated at the front and unites the dental plates. x 2.
Silurian (Gotlandian), Visby, Gotland, Sweden. Riks. Pal. Zool. Avd., Stockholm.

FIGS. *Linoporella punctata* (Verneuil)—Cont.

- 24.—Reverse side of exterior in fig. 33, showing well inter-area, teeth, dental plates, and median ridge. x 1.5.
- 33.—Exterior of a large ventral valve, showing characteristic ornamentation. x 1.5.
Silurian (Gotlandian), Visby, Gotland, Sweden. Riks. Pal. Zool. Avd., Stockholm.
- 17.—Posterior portion of large dorsal valve, showing cardinalia. Note extremely slender shaft of cardinal process, with its thickened unlobed myophore. Brachio-phore plates uniting below with median septum to form a cruralium.
Silurian (Gotlandian), Föro, Lausa, Sweden. x 2.

Levenea subcarinata (Hall)

- 19, 32.—Dorsal interiors, the former, x 1.5, showing adventitious growths on inside of brachio-phores, and the latter, x 2, showing well musculature and pallial marks.
- 31.—Ventral interior, showing characteristic musculature. x 1.5.
Devonian (Birdsong), Birdsong Creek, west Tennessee. Cat. No. S 982.
- 20.—Enlargement of fig. 28, x 3.
- 28.—Dorsal interior, turned slightly to the side, showing unmodified brachio-phores in the form of flat, obliquely placed blades. x 1.5.
Devonian (Helderberg). Albany Co., N. Y. Cat. No. S 986.
- 21.—Dorsal interior, showing greatly modified interior. Shaft of cardinal process modified by a process growing forward from median lobe of myophore, brachio-phores coated on inside by adventitious material which cements them to the valve. Lateral pallial sinuses given off between adductor impressions clearly visible.
Devonian (Birdsong), near Holladay, Tenn. Cat. No. S 980. x 1.5.
- 23.—Dorsal interior of young individual, showing brachio-phores as simple, unmodified, oblique blades. x 1.5.
- 25, 29.—View, x 1.5, and its enlargement, x 3.5, to show modified brachio-phores, a line of demarcation between actual plates and adventitious substance being clearly visible.
Devonian (Birdsong) Conrad Place, near Jeanette, Tenn. Cat. No. S 988.
- 30.—Ventral internal mold, showing pentagonal form of muscle field and pallial markings.
Devonian (Helderberg), near Clarksville, N. Y. Cat. No. S 1014. x 1.5.

Levenea cf. subcarinata (Hall)

- 22, 26, 27.—Posterior, ventral, and dorsal exterior views.
Devonian (Birdsong), Benton Co., Tennessee. Cat. No. 9719 Y. P. M. x 1.5.

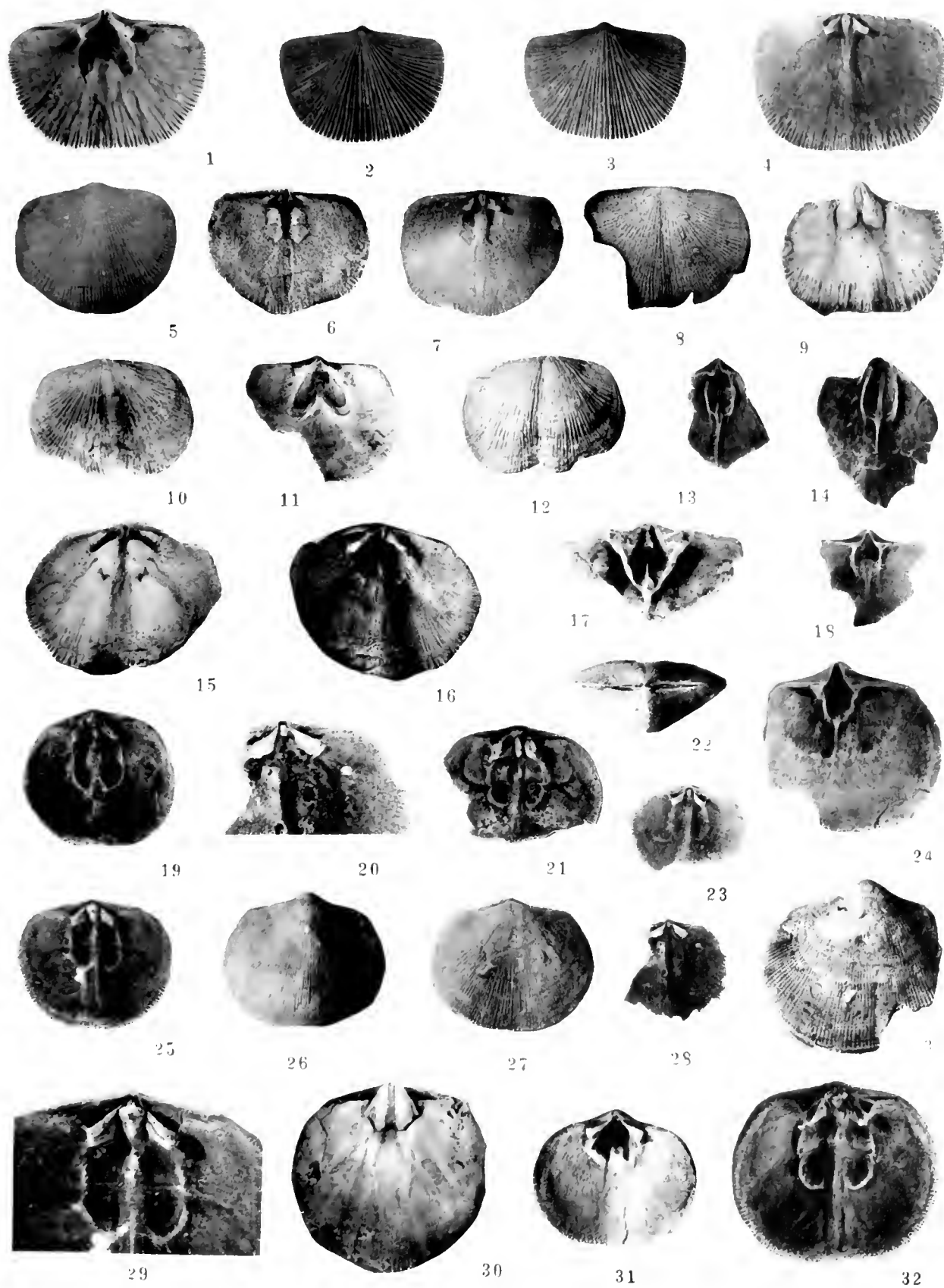


PLATE 19

FIGS. *Thiemella villenovia* Williams

- 1, 5.—Dorsal and ventral exterior views, showing well the reversion of fold and sulcus which is one of the generic characters. The specimens figured are squeezes of external molds in the U. S. Nat. Mus. x 1.5.
- 2, 6.—Ventral internal molds, showing musculature and long septum dividing anterior ends of diductor scars and extending some distance in front of them. Fig. 2 x 1.5, fig. 6 x 2.
- 4.—Replica of dorsal internal mold, showing cardinalia. x 1.5. Note delicacy of structures and compare with the rather ponderous cardinalia of *Aulacella*, fig. 13.
- 9.—Dorsal internal mold, the reverse side of that in fig. 4. x 1.5.
- Devonian (Chemung), Dyes quarry, Villenova, Chautauqua Co., N. Y. Originals in U. S. Nat. Mus.

Rhipidomella vanuxemi (Hall)

- 3.—External view of ventral valve, showing swollen costellæ.
- Devonian (Hamilton), Canandaigua Lake, N. Y. Cat. No. S 1286. x 1.

Aulacella eifelensis (Verneuil)

- 7, 8.—Dorsal and ventral views of exterior, showing fold and sulcus, which are not reversible. x 1.5.
- 11.—Ventral internal mold, showing musculature. Adjustor impressions clearer in this specimen than usual. Cf. the same view of *Thiemella*, fig. 6, and note that whereas in *Aulacella* the septum forks at the ends of the diductor scars, in *Thiemella* there is no forking and the septum extends a considerable distance in front of the muscle field. x 2.
- Mid. Devonian, Eifel, Germany. Cat. No. S 1096.
- 10.—Ventral interior, showing elongate muscle field with diductor impressions separated by a low ridge which forks in front. x 2.
- 13.—Dorsal interior, showing ponderous cardinalia which have a strong resemblance to those of *Rhipidomella*. Cf. fig. 4. x 1.5.
- Mid. Devonian, Eifel, Germany. Schultze Colls., Mus. Comp. Zool., Harvard Coll.

Perditocardinia dubia (Hall)

- 12, 20, 22.—Lateral, dorsal, and ventral views of a large specimen, showing terebratuloid form of valves.
- 21.—Ventral interior, showing musculature.
- Mississippian (St. Louis), Spargen Hill, Ind. Cat. No. S 1300. x 2.
- 16, 17.—Ventral and posterior views of exterior.
- Mississippian (Carthage), Webb City, Jasper Co., Missouri. Cat. No. S 1293. x 2.

FIGS. *Perditocardinia* aff. *P. dubia* (Hall)

- 14, 15.—Ventral and dorsal interiors. Ventral interior shows clearly the lack of an interarea and consequently of a hinge-line. Dorsal interior shows ponderous cardinalia similar to those of *Rhipidomella* but with modifications induced by the compression of the interarea to disappearance.
- Mississippian (Salem), near Valley Park, St. Louis Co., Missouri. Cat. No. S 1297. x 2.

Platyorthis planoconvexa (Hall)

- 18, 19, 29.—Dorsal, ventral, and lateral exterior views. Notice particularly planoconvex profile. x 1.
- 23.—Ventral interior, showing flaring dental plates continued as ridges along margins of muscle field. x 1.5.
- 24.—Dorsal interior of silicified specimen, showing ponderous cardinal process and oblique, blade-like brachio-phores. x 1.5.
- Devonian (Oriskany), Cumberland, Md. Cat. No. S 1145.

Platyorthis circularis (Sowerby)

- 27.—Dorsal internal mold. The pit marking the cardinal process is short, showing a short cardinal process but elevated a considerable distance in a ventral direction.
- 28.—Ventral internal mold, showing elongate flabellate adjustor-diductor fields separated by a median ridge which carried the adductor muscles.
- Devonian (Coblentzian), Siegen, Germany. Cat. No. S 1139. x 1.5.

Platyorthis opercularis (Verneuil)

- 31.—Dorsal view of exterior, showing flatness of dorsal valve.
- Devonian (Eifelian), Gerolstein, Germany. Cat. No. S 1141. x 1.5.

Proschizophoria personata (Zeiler) (emend. Kayser)

- 25.—Dorsal internal mold. Cardinal process and brachio-phore plates ponderous. Anterior adductor impressions separated from posterior impressions by horizontal ridges (in the mold, depressions).
- 30.—Ventral internal mold, showing subtriangular muscle field. Diductor impressions long and adductor impressions imprisoned within them.
- Up. Devonian, Unkel, Germany. Schultze Colls., Mus. Comp. Zool., Harvard Coll. x 1.
- 26, 32.—Ventral and dorsal internal molds.
- Low. Devonian (Siegenerschichten), Seifen, Germany. Cat. Nos. S 1090 and S 1089. x 1.5.

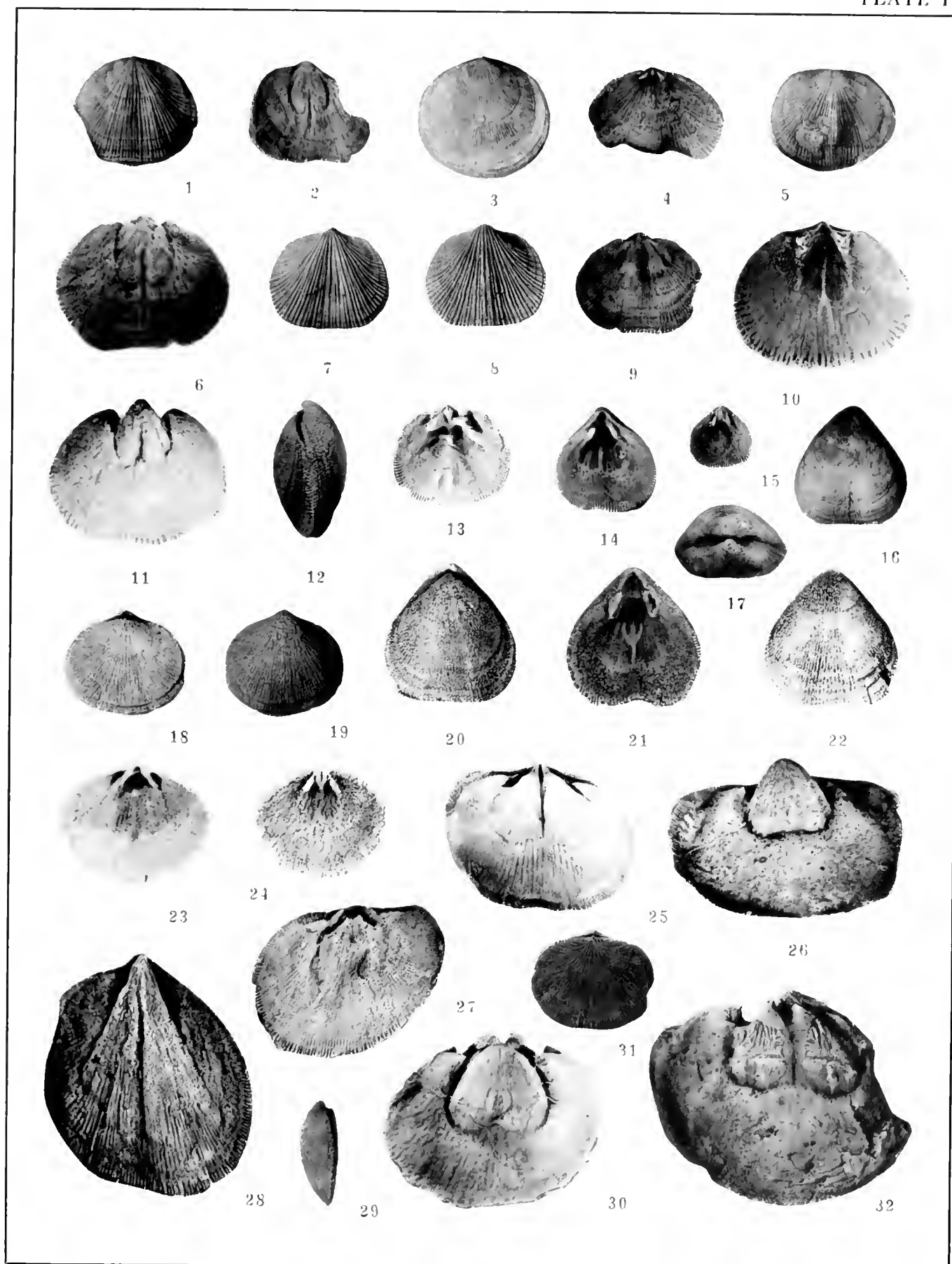


PLATE 20

FIGS. *Smeathenella harnagensis* Bancroft

- 1, 5.—Dorsal internal mold, and a replica of it which shows brachiophores cemented to valve to produce thornlike structures. Cf. fig. 19, *Heterorthis clytie*.
 - 2, 4.—Internal mold of crushed ventral valve, and a replica taken from it, to show short dental plates.
 - 3.—Replica taken from dorsal exterior mold, showing fascicostellate surface.
- Ordovician (basal Harnagian), Smeathen Wood, Horderley, E. Shropshire, England. Cat. Nos. S 2119, S 2120. x 1.

Harknessella vesperilio (Sowerby)

- 6, 10.—Ventral internal mold (10), and replica. Muscle area lobate.
 - 7, 9.—Dorsal internal mold (9), and replica. This wax impression shows clearly the nature of the brachiophores, although the lobate character of the cardinal process is not altogether clear because of the imperfection of the impression. The cementing of the brachiophores to the valve is clear, however. Cf. fig. 19.
- Ordovician (basal Caradocian, *Heterorthis patera* grits), Coston District, E. Shropshire, England. Cat. Nos. S 2122 (figs. 6, 10) and S 2123. x 1.

Harknessella sp.

- 8.—Dorsal internal mold.
- Ordovician (basal Caradocian, *Harknessella subquadrata* zone), Bullhill, Cressage District, E. Shropshire, England. Cat. No. S 2124. x 1.

Reuschella bilobata (Sowerby)

- 11, 14.—Ventral internal mold (14) and wax impression taken therefrom, showing character of muscle field.
 - 13, 15.—Dorsal internal mold, and replica. Cardinalia close to those of *Harknessella*.
- Ordovician (Acton Scott beds), Castle Hill, E. Shropshire, England. Cat. Nos. S 2125 (figs. 13, 15) and S 2126. x 1.

Reuschella cf. *R. bilobata* (Sowerby)

- 12.—Dorsal exterior, showing coarse costellæ.
- Ordovician (Caradocian), Cardington, Salop, England. Cat. No. S 1065. x 1.

Heterorthis clytie (Hall)

- 16, 17.—Ventral and dorsal views of exterior.
- Ordovician (Trenton), Bourbon Co., Ky. Cat. No. S 1068. x 1.5.

FIGS. *Heterorthis clytie* (Hall)—Cont.

- 18.—Dorsal interior, showing cardinalia. x 1.5.
 - 19.—Posterior view of specimen in fig. 20, showing small, convex chilidium covering carinate median lobe of cardinal process. x 2.
 - 20.—Dorsal interior, showing cardinalia, small adductor field, and pallial marks; also cementation of brachiophores to valve. In *Heterorthis* and its allies this cementation takes place along the dorsal surface of the brachiophores, but in *Dalmanella*, *Levenea*, etc., it is along their flat, inner face. Shown also in this figure is the submarginal elevation in the dorsal valve, and the corresponding depression in the ventral valve can be seen in fig. 21. x 1.5.
 - 21.—Ventral interior, showing semiflabellate pattern formed by combined diductor and adjustor scars. x 1.5.
- Ordovician (Hermitage), Frankfort, Ky. Cat. Nos. S 1067 (figs. 19-21) and S 1074.

Heterorthis cf. *H. alternata* (Sowerby)

- 25.—Ventral internal mold, showing elongate diductor and adjustor muscles.
- Ordovician (Caradocian), W. Corwan, England. Cat. No. S 1073. x 1.5.

Rhipidomella sp.

- 22.—Dorsal interior turned slightly to the side showing cardinalia. Right brachiophore shows an elongate blade-like process extending from a median swelling. Such a process is missing in fig. 23.
- Locality unknown. Cat. No. S 1220. x 3.

Rhipidomella vanuxemi (Hall)

- 23.—Dorsal interior, showing swollen cardinal process and adductor field.
 - 27.—Ventral interior, showing postero-median position of adductor field, and large, semiflabellate diductor-adjustor area.
- Devonian (Hamilton), Canandaigua, N. Y. Cat. No. S 1286. x 1.5.

Rhipidomella musculosa (Hall)

- 24.—Ventral interior, showing unusually expansive development of diductor-adjustor fields.
- Devonian (Oriskany), Cumberland, Md. Cat. No. S 1193. x 1.

Rhipidomella penelope (Hall)

- 26.—Ventral interior of an old shell, showing puckered margins of muscle field and swollen, irregular inner surface.
- Devonian (Hamilton), Canandaigua Lake, N. Y. Cat. No. S 1229. x 1.



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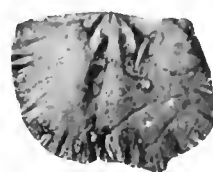
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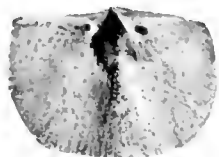
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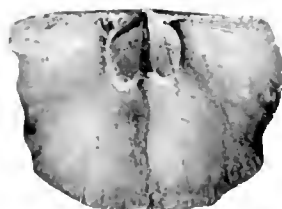
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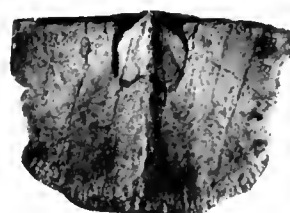
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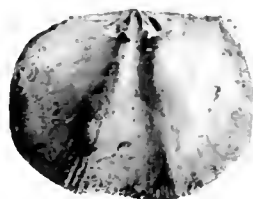
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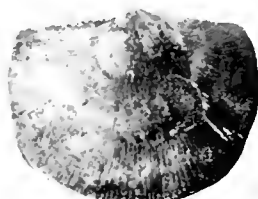
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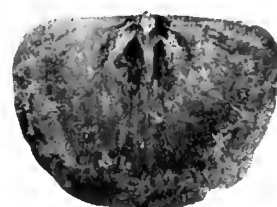
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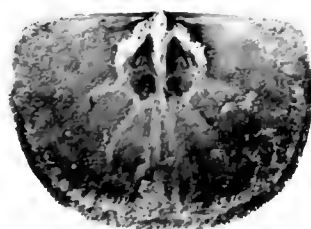
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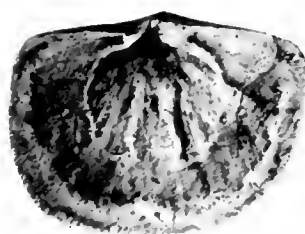
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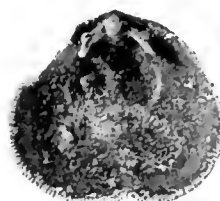
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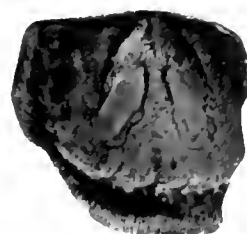
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PLATE 21

FIGS. Aff. *Parmorthis visbyensis* (Lindström)

- 1, 6, 12.—Dorsal, ventral, and posterior views of a medium-sized individual.
 8.—Dorsal interior, showing adductor field and trilobed cardinal process. The concavity of the dorsal valve has caused a bending postero-dorsally of the cardinal process in order to maintain the necessary leverage in opening the valves. This makes the myophore visible on the exterior of the dorsal valves (see fig. 1).
 11.—Dorsal view of a larger shell.
 15.—Ventral internal mold, showing pallial trunks swinging into apposition as they extend forward. This is the usual condition in *Parmorthis* and is a significant difference between these shells and *Dalmanella s. s.* Silurian (Gotlandian), Gotland, Sweden. Cat. No. S 895. x 2.

Parmorthis elegantula (Dalman)

- 2.—Dorsal interior seen from rear, showing (on left brachiophore) an elongate process or crus (?).
 3.—Posterior view of a dorsal interior, showing fulcral plates and brachiophores. *Parmorthis* is the only dalmanellid with corrugated dental sockets, teeth, and fossettes.
 13.—Dorsal interior, showing elongate-ovate adductor field with its smaller anterior adductor scars. Fulcral plates visible, and inside surface of brachiophores strengthened by adventitious material. Silurian (Gotlandian), Gotland, Sweden. Cat. Nos. S 886 (fig. 2) and S 892. x 2.
 9, 14, 16.—Posterior, dorsal, and ventral views of exterior. In fig. 14, a concentration of smaller costellæ is noticeable in the antero-median portion of the valve. Such a concentration of ribs is a feature of these shells.
 10, 29.—Two views of a ventral interior, showing ponderous teeth and cavernous crural fossettes. Silurian (Gotlandian), Klintehamn, Gotland, Sweden. Cat. Nos. S 890 (figs. 9, 14, 16), and S 918. x 2.

Parmorthis crassicostata Schuchert and Cooper, n. sp.

- 4, 5.—A rather heavily costellate species. Silurian (Niagaran), Martin's Mills, W. Tenn. Holotype. Cat. No. S 913. x 2.

Parmorthis waldronensis (Foerste)

- 7.—Ventral exterior of the common American shell that has so long masqueraded under the name of *Dalmanella elegantula* (Dalman). Silurian (Niagaran), Jefferson Co., Ind. Cat. No. S 899. x 2.

Isorthis perelegans (Hall)

- 17, 18.—Dorsal and lateral views of exterior, the latter showing biconvexity of valves.
 26.—Ventral interior, showing *Schizophoria*-like muscle-scars.
 28.—Dorsal interior, showing cardinalia. Devonian (Helderberg), Clarksville, N. Y. Cat. No. S 1013. x 1.

FIGS. *Isorthis rockhousensis* (Dunbar)

- 19.—Dorsal exterior. Low. Devonian (Rockhouse), Rockhouse, Tenn. Cat. No. 9750 Y. P. M. x 2.

Isorthis szajnochai Kozłowski

- 20.—Posterior portion of a dorsal valve, showing divergent diductor tracks and median adductor fold. This is very similar to the condition in *Schizophoria*, see pl. 23, fig. 20. x 2.
 25, 30, 31, 33.—Ventral, dorsal, posterior, and lateral views of a specimen representing the type species of the genus. x 1.5.
 27.—Dorsal interior, showing cardinalia and adductor field. Fulcral plates visible just outside brachiophore plates. Cf. corresponding view of *Schizophoria*, pl. 23, fig. 21. x 1.5.
 Up. Silurian (Borszczów), Wierzchniakowce, Poland. Cat. No. S 2127.

Isorthis arcuaria (Hall and Clarke)

- 21.—Dorsal interior, showing elliptical adductor field and prominent ridges of adventitious shell extended around it.
 23.—Ventral interior, showing prominent divergent diductor tracks and pallial sinuses extending from them. Diductor tracks separated by a fold of shell which bears adductor impressions. Silurian (Niagaran), Decatur Co., W. Tenn. Cat. No. S 1030. x 2.
 32.—Lateral view, showing strongly lenticular profile of shell. Silurian (Niagaran), Clifton, W. Tenn. Cat. No. S 1022. x 2.

Isorthis tetragonum (Roemer)

- 22.—Dorsal internal mold, to show pallial markings. Devonian (Eifelian), Gerolstein, Germany. Cat. No. S 994. x 1.5.

Isorthis canalicula (Schnur)

- 24.—Ventral interior, with musculature and pallial markings characteristic of the genus. Devonian, Eifel, Germany. Mus. Comp. Zool., Harvard Coll. x 2.

Idiorthis matura McLearn

- 34.—Ventral internal mold, showing musculature. Cf. *Wattsella*, pl. 22. x 3.
 35, 38.—Dorsal and ventral views of exterior. x 1.5.
 36, 37.—Dorsal internal mold (37), x 1.5, and replica of it showing strong median ridge and adductor field. Cardinal process trilobed. Silurian (McAdam), Arisaig, Nova Scotia. Cat. Nos. 426 (figs. 34, 36, 37) and 426c Y. P. M.



PLATE 22

Mendacella uberis (Billings)

- 1.—Dorsal interior, showing cardinalia.
- 2.—Ventral interior, showing musculature.
- 3.—Dorsal internal mold, showing elongate *Dalmanella*-like muscle field.
Ordovician (Richmond, Ellis Bay), E. of Junction Cliff, Anticosti. Cat. No. 10415 Y. P. M. x 2.
- 8.—Ventral exterior.
Silurian (Anticostian), Anticosti. Cat. No. S 1049. x 2.

Mendacella mullochiensis (Davidson)

- 4, 5.—Ventral internal mold (fig. 5), x 1.5, showing musculature, and wax impression taken from it, x 2.
Silurian (lower Llandovery, Mulloch Hill), Mulloch Hill, Girvan, Ayrshire, Scotland. Brit. Mus. Nat. Hist. (fig. 5); Cat. No. S 657 (fig. 4).

Fascicostella sedgwicki (D'Archiac and Verneuil)

- 6.—Dorsal internal mold, showing adductor field like that of *Parmorthis*, see pl. 21, fig. 13.
- 7.—Ventral exterior, showing bundled costellæ.
- 10.—Replica of interior.
- 11.—Dorsal interior, showing cardinalia.
- 16.—Reverse side of fig. 6, showing ventral interior mold.
Of significance is the septum extending forward from the adductor track separating two pallial trunks.
Devonian, Visé, Belgium. Mus. Comp. Zool., Harvard Coll. x 2.

Fascicostella gervillei (Defrance)

- 12, 15.—Ventral and dorsal exteriors, showing fascicostellate exterior.
Devonian (Ff₂), Konicpruss, Bohemia. Cat. No. S 925. x 1.5.

Fascicostella sp.

- 31.—Large specimen, showing dorsal exterior.
Devonian, Visé, Belgium. Mus. Comp. Zool., Harvard Coll. x 2.

Wattsella edgewoodensis (Savage)

- 9, 23, 25, 29.—Several views to show dorsal interior. Fig. 23 shows left brachiophore plate broken away to obtain a clearer view of the right plate. Fig. 29 is an enlargement of fig. 23, x 4. Fig. 25 shows socket and fulcral plates.
Silurian (Edgewood), Edgewood, Pike Co., Missouri. Cat. Nos. S 1078 (figs. 23, 25, 29), S 1079 (fig. 9). All except fig. 29 x 2.

FIGS. *Wattsella edgewoodensis* (Savage)—Cont.

- 13.—Ventral interior, showing flaring dental plates and heart-shaped muscle field.
- 22.—Dorsal interior of a silicified shell, showing remarkably long brachiophores (crura?).
- 27, 28.—Dorsal and ventral exteriors, to show ornamentation.
Silurian (Edgewood), Edgewood, Pike Co., Missouri. Cat. Nos. S 1075 (figs. 13, 27, 28), and S 1083 (fig. 22). x 2.

Wattsella testudinaria (Dalman)

- 14, 19, 24.—Posterior, ventral, and dorsal exteriors. x 1.5.
- 21.—Dorsal interior, showing subparallel brachiophore plates, meeting the median ridge. x 2.
Silurian, Borenshult, Sweden. Riks. Pal. Zool. Avd. Stockholm.

Wattsella watti Bancroft

- 17.—Ventral exterior, a replica of the internal mold.
- 18, 20.—Dorsal internal mold, and wax replica of it, showing subparallel brachiophore plates meeting median ridge. Cf. figs. 21, 9, and 23.
- 26.—Ventral internal mold, showing subcordate muscle area.
Ordovician (Marshbrookian, *W. watti* zone), Woolston, Horderley District, E. Shropshire, England. Cat. Nos. S 2128 (fig. 17), S 2129 (figs. 18, 20), and S 2130 (fig. 26). x 1.5.

Horderleyella sp.

- 30.—Dorsal interior, showing fulcral plates outside brachiophore plates.
Ordovician (Marshbrookian, *Wattsella watti* zone), Marshbrook, N. of Horderley, E. Shropshire, England. x 1.5.

Horderleyella plicata Bancroft

- 32.—Ventral internal mold.
- 33.—Wax replica of dorsal external mold.
- 34, 35.—Dorsal internal mold (fig. 35) and wax replica of it showing cardinalia. Brachiophore plates convergent and supported by low lateral septa.
Ordovician (basal Caradocian, *H. plicata* zone), Horderley, E. Shropshire, England. Cat. Nos. S 2132-2134. x 2.

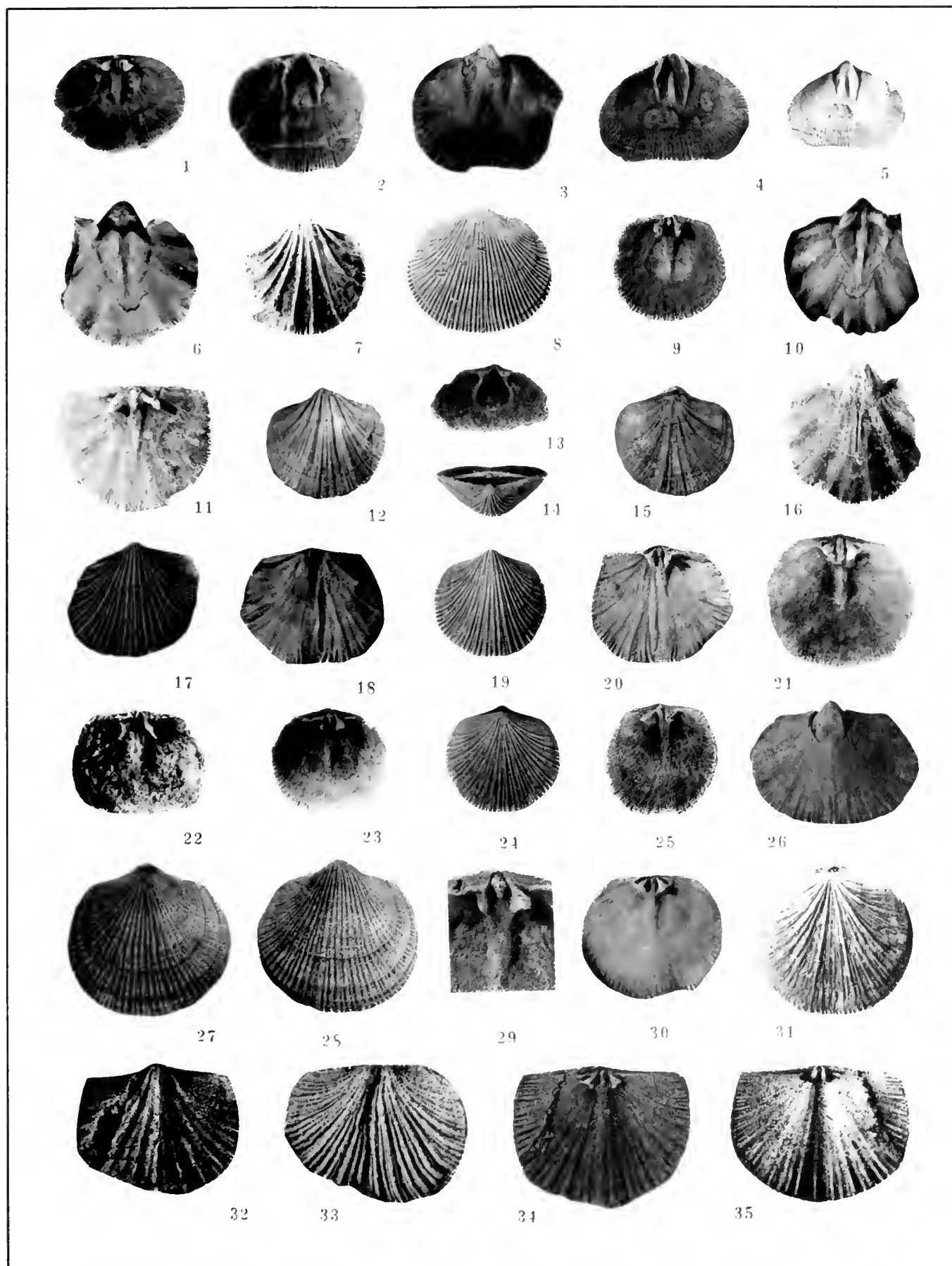


PLATE 23

FIGS. *Pionodema subæquata* (Conrad)

- 1, 5.—Ventral and dorsal views of the holotype.
Ordovician (Black River), Mineral Point, Wis.
Cat. No. 694/3 Amer. Mus. Nat. Hist. x 2.
- 3.—Posterior view of exterior. x 1.5.
- 7.—Dorsal interior, showing flaring brachiophore plates and thickenings extending forward from them. Cf. figs. 2, 4. x 3.
Ordovician (Black River), near Lanesboro, Minn.
Cat. No. S 1364.

Pionodema redux (Barrande)

- 2, 4.—Dorsal internal mold (fig. 4) and wax impression of it. Cf. fig. 7. Brachiophore plates separate, but low ridges extend from them and converge toward the median ridge.
Ordovician (D_d), Mt. Drabow, Bohemia. Mus. Comp. Zool., Harvard Coll. x 1.5.

Pionodema minnesotensis Cooper

- 6, 10, 14.—Dorsal, ventral, and posterior views of the holotype. Notice swollen ribs.
Ordovician (Black River), Minneapolis, Minn.
Cat. No. S 1356. x 1.5.

Pionodema cf. *circularis* (Winchell)

- 8.—Dorsal interior, showing well the flaring brachiophore plates. Cf. fig. 21.
Ordovician (Glade ls. of Safford (?)), Lebanon, Tenn. Cat. No. S 1360. x 2.

Pionodema cf. *conradi* (Winchell)

- 9.—Ventral interior, showing musculature and apical plate.
Ordovician (Black River), St. Paul, Minn. Cat. No. 1359 S. x 1.5.

Pionodema uniplicata Cooper

- 12.—External view of ventral exterior, showing deep sulcus.
Ordovician (Black River), Minneapolis, Minn.
Cat. No. S 1361. x 1.5.

FIGS. *Pionodema circularis* (Winchell)

- 13.—Incomplete dorsal valve turned to the side in order to show the fulcral plate which defined the socket. Cf. fig. 18.
Ordovician (Black River), 2.5 miles S. of High Bridge, Ky. Cat. No. S 1348. x 3.

Isorthis ? tulliensis (Vanuxem)

- 15, 19.—Ventral internal mold, and reverse side showing dorsal interior. Pallial marks distinctly spread apart, showing pattern clearly.
Devonian (Tully), Skaneateles, N. Y. Cat. No. S 1412. x 1.5.

Schizophoria provulvaria Maurer

- 11.—Dorsal internal mold, showing pallial trunks.
Devonian, Seifen, Germany. Cat. No. S 1401. x 1.

Schizophoria vulvaria (Schlotheim)

- 16.—Ventral internal mold, showing exceedingly long diductor impressions separated by a long septum.
- 17.—Dorsal interior, showing pallial markings.
Low. Devonian (Coblenzian), Laubach, Germany.
Mus. Comp. Zool., Harvard Coll. x 1.

Schizophoria iowensis (Hall)

- 18.—Same specimen as in fig. 21, turned to side to show brachiophore supports and fulcral plates.
- 20.—Ventral interior, showing musculature and median fold which carries adductor impressions.
- 21.—Dorsal interior, showing flaring brachiophore plates, fulcral plates, and musculature.
Up. Devonian, Rockford, Iowa. Cat. No. S 1441. x 2.

Schizophoria aff. *striatula* (Schlotheim)

- 22-25.—Posterior, dorsal, lateral, and ventral views of exterior. Compare fig. 24 with fig. 19 of pl. 11.
Devonian (Craghead Creek), E. of Toledo, Callaway Co., Missouri. Cat. No. S 1447. x 1.

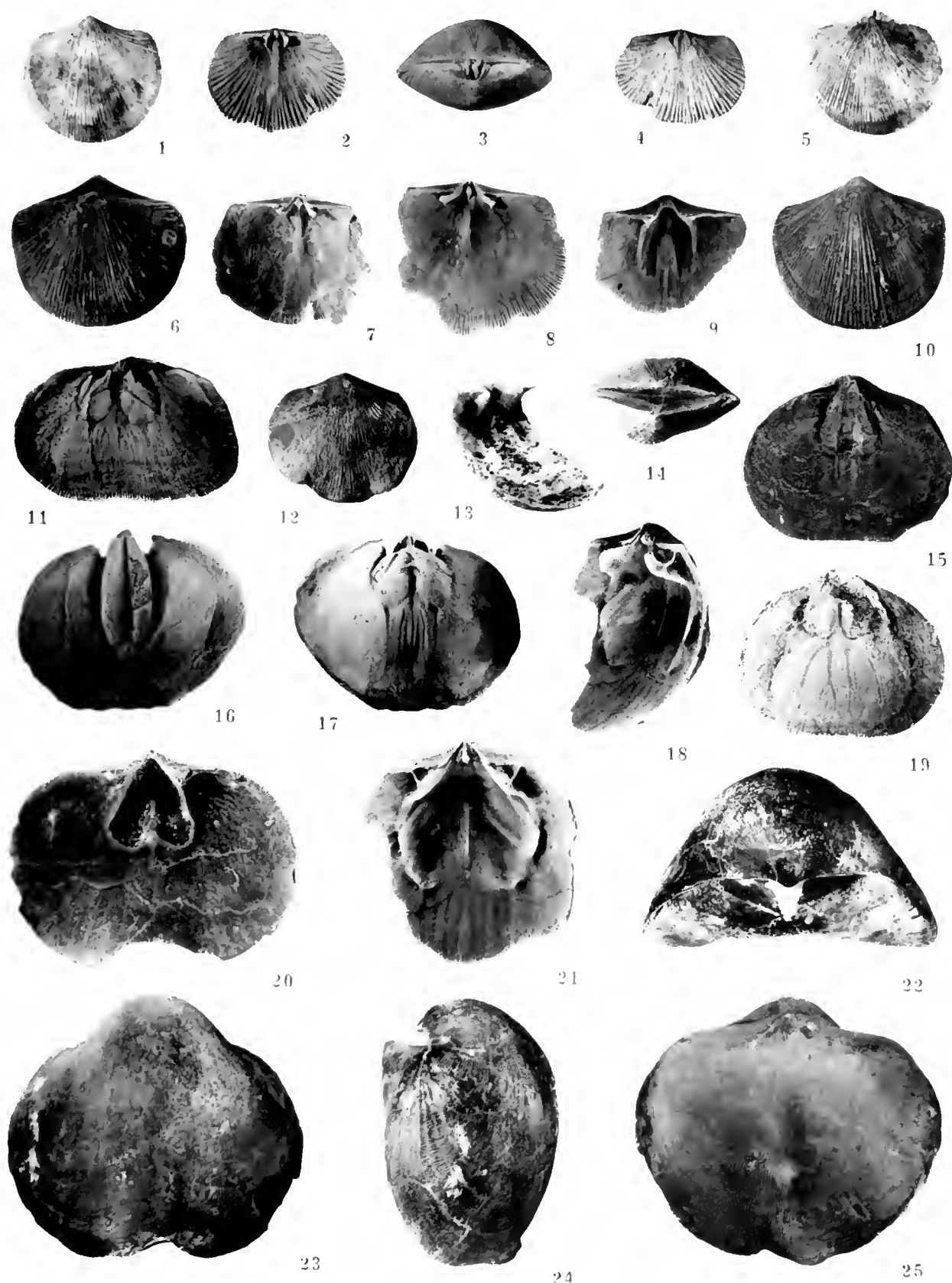


PLATE 24

FIGS. *Enteleles lamarcki* Fischer

- 1, 5, 8, 9.—Dorsal, ventral, posterior, and lateral views of exterior, showing fine *Schizophoria* ornamentation superimposed over plications.
Up. Carboniferous, Mjatschkowa, Russia. Cat. No. S 1495. x 1.

Enteleles dumblei Girty

- 2, 6, 10.—Ventral interior, showing three prominent septa, x 1.5. Figs. 2 and 6 seen from the side.
3.—Dorsal interior, showing flaring brachiophore supports and curved brachiophores, x 2.
7.—Small interarea of ventral valve, x 1.5.
Pennsylvanian (Word), Glass Mts., W. Texas. Fig. 2 is Cat. No. S 2224, the others are specimens in the Univ. of Texas collections.

Enteleles cf. dumblei Girty

- 25.—Dorsal valve seen from the side, showing tusklike brachiophores and a fulcral plate in place.
Permian (Wolfcamp), N. E. of Wolfcamp, Glass Mts., W. Texas. Cat. No. S 1501. x 3.

Parenteleles cooperi King

- 11, 13, 18.—Anterior, lateral, and posterior views of exterior, showing strong ventral fold and ornamentation of an adult.
14, 16.—Ventral and dorsal views of exterior of a young specimen.
Pennsylvanian (Gaptank), near Gaptank, Glass Mts., W. Texas. Univ. Texas colls.

FIGS. *Parenteleles cooperi* King—*Cont.*

- 21, 26.—Ventral interior of cotypes, showing septa and camera under anterior end of median septum.
Permian (Uddenites zone), Hill 4752, Glass Mts., W. Texas. Cat. No. S 1494. x 2.

Enteletella nikschitschi Likharev

- 4.—Lateral view of a complete individual, after Likharev.
Low. Permian, northern Caucasia.

Orthotichia aff. *morganiana* (Derby)

- 12.—Extreme posterior portion of dorsal valve, showing cardinal process and a complete brachiophore. x 1.5.
15.—Posterior portion of a ventral valve, showing elevated median septum. x 2.
22.—Ventral view, with shell worn off, showing three septa, x 1.
23, 24, 27.—Posterior, ventral, and dorsal exterior views. x 1.
Pennsylvanian, near Saddle Mt., S. E. of Winkelman, Ariz., near Gila River. Cat. No. S 1493.

Enteletina latesinuata (Waagen)

- 17.—Ventral interior, showing subparallel dental plates and simple median septum. Cf. fig. 10.
19.—Ventral exterior, showing prominent fold.
20.—Dorsal interior. Shape of brachiophore process normal, but lateral curvature undoubtedly incorrect.
Middle Productus ls., Musakheyl, India. All after Waagen 1887.

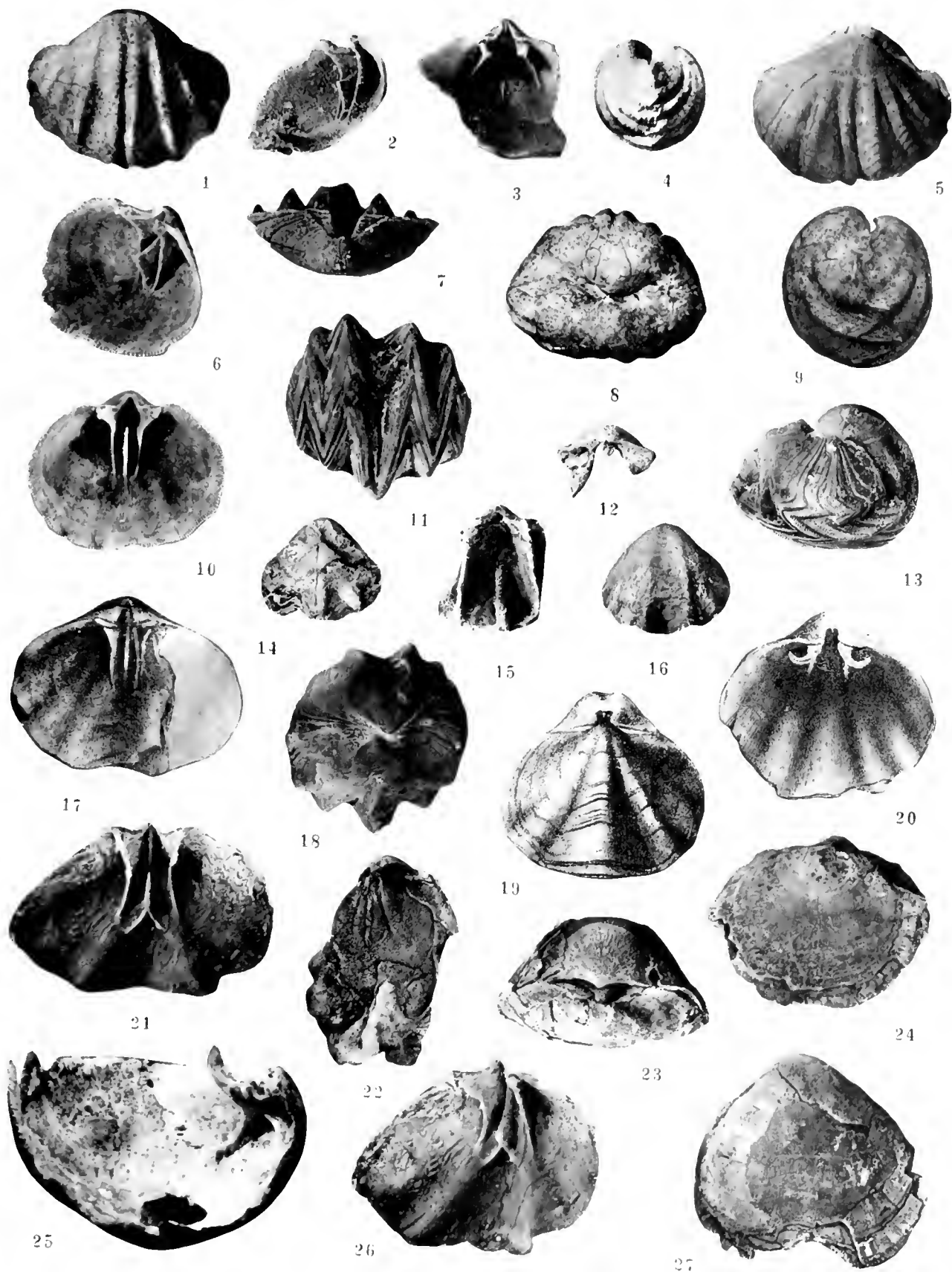


PLATE 25

FIGS. **Rhynchocamara plicata** Schuchert and Cooper

- 1, 2, 7.—Ventral, posterior, and dorsal views of exterior, showing subrhynchonelloid form.
 17.—Posterior portion of ventral interior, showing spondylium.
 18.—Dorsal interior, showing small chamber beneath beak of dorsal valve, formed by union of crural plates with strong median septum. This is a rhynchonelloid feature and places this form and its congeners with the Rhynchonellacea.
 Ordovician (Stones River, Central ls.), near Murfreesboro, Tenn. Cotypes. Cat. No. S 2035. x 1.5.

Camerella hemiplicata (Hall)

- 3, 4, 6, 10.—Posterior, ventral, lateral, and dorsal views of a somewhat crushed specimen, showing strongly convex dorsal valve and relatively smaller ventral valve. x 1.
 43.—Thin slice of interior, showing spondylium, cruralium, and crural alæ. x ca. 4.
 Ordovician (Trenton), Lowville, N. Y. Cat. Nos. S 1593 and S 1597 (fig. 43).
 9, 11.—Ventral and anterior views, showing sulcus. x 1.
 16.—Ventral view of a young shell, showing median septum. x 1.
 24.—Section of interior of a rather young form, showing spondylium and cruralium. A faint crural alar extension can be seen. x 4.
 Ordovician (Trenton), Watertown, N. Y. Cat. Nos. S 1588 (figs. 9, 16), S 1600 (fig. 11), and S 1603 (fig. 24).

Camerella volborthi Billings

- 5.—Ventral interior, with prominent spondylium.
 Ordovician (Black River), Paquette Rapids, Ottawa River, Quebec. Cat. No. 1594 S, x 1.5.
 20, 21.—Ventral and dorsal views of a young specimen.
 27, 30.—Lateral and dorsal views of a larger individual. These specimens were among Billings' types.
 Same horizon and locality as above. Cat. Nos. 1148b, 1148a, Nat. Mus. Canada. x 2.
 22, 28, 29.—Lateral, dorsal, and posterior views of the same individual, showing exterior. Cf. *C. hemiplicata*, especially fig. 9.
 Same horizon and locality as above. Nat. Mus. Canada. x 2.

FIGS. **Camerella scofieldi** (Winchell and Schuchert)

- 8, 12, 13.—Ventral, posterior, and dorsal views of exterior.
 Ordovician (Galena), near Cannon Falls, Minn. Cat. No. S 1592. x 1.

Anastrophia verneuili (Hall)

- 14, 15, 19.—Lateral, posterior, and dorsal views of exterior, showing implantation of ribs in fold. x 1.
 Devonian (Helderberg), near Clarksville, N. Y. Cat. No. S 1619.
 33, 36.—Dorsal interior, showing partial side and dorsad views. Fig. 36 shows musculature well. x 1.5.
 34, 35.—Spondylium in partial side and direct or dorsad view. Septum supports spondylium for nearly its whole length. x 1.5.
 38, 39.—Different views of the same specimen, showing to perfection crural alæ, supporting plates, and musculature. x 1.5.
 Devonian (Helderberg), Clarksville, N. Y. Cat. No. S 1640.
 41.—Interior of both valves in conjunction. x 1.5.
 42.—Same view of another specimen, in which the sides of the spondylium have grown over, restricting the area of muscular attachment to a narrow opening. x 1.5.
 Devonian (Helderberg), near Clarksville, N. Y. Cat. Nos. S 1632 (fig. 41) and S 1631.

Anastrophia deflexa (Sowerby)

- 40.—Thin section, showing arrangement of internal plates. There are lateral alæ on the spondylium as well as in the dorsal valve.
 Silurian (Wenlock), Dudley, England. Cat. No. S 1623. x ca. 4.

Parastrophinella ops (Billings)

- 23, 25, 26.—Ventral, posterior, and dorsal views of exterior.
 Silurian (Chicotte), Anticosti. Cat. No. S 1608. x 1.

Liocœlia proxima (Barrande)

- 31, 32, 37.—Ventral, dorsal, and lateral views of exterior of this smooth rhynchonellid. See t. fig. 36.
 Silurian (Etage Ee₂), Kolednik, Bohemia. Cat. No. S 1696. x 1.

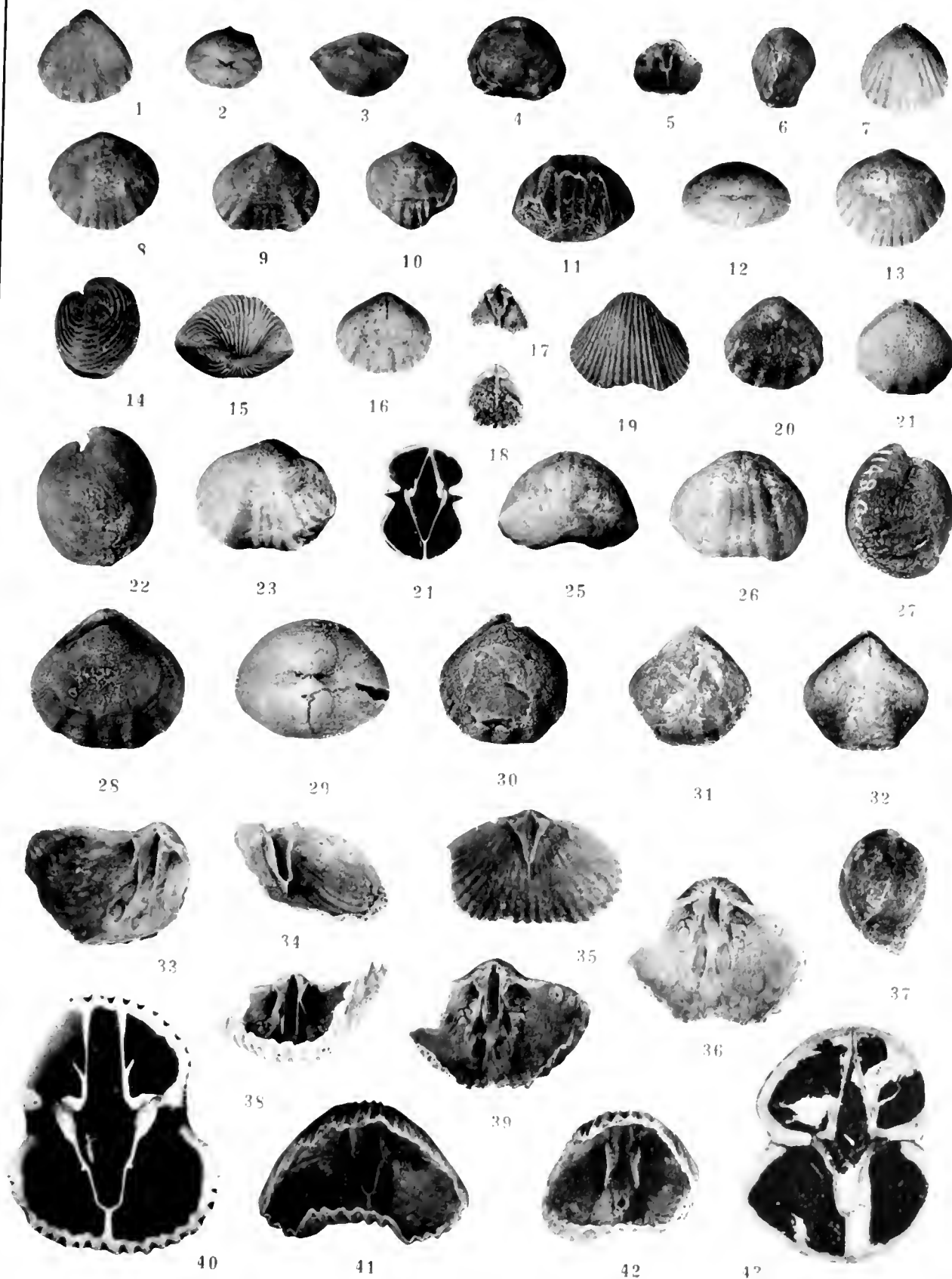


PLATE 26

FIGS. *Barrandella linguifera* (Sowerby)

- 1, 3, 5, 6.—Dorsal, ventral, posterior, and lateral views of a complete individual.
Silurian (Gotlandian), Gotland, Sweden. Cat. No. S 1680. x 1.

Barrandella sp.

- 2, 7.—Dorsal and posterior views of an internal mold, showing septa.
Silurian (Brassfield), Eaton, Ohio. Cat. No. S 1674. x 1.

Pentamerella cf. *arata* (Conrad)

- 4.—Dorsal interior, showing long plates of dorsal valve which carry brachial processes.
17.—Ventral interior, showing spondylium. Septum very short.
Devonian (Onondaga), Falls of the Ohio, Louisville, Ky. Cat. No. S 1731. x 1.5.
13.—Ventral interior, showing short spondylium and two pallial trunks.
Devonian, Moreland, Ky. Cat. No. S 1726. x 1.

Pentamerella arata (Conrad)

- 20.—Dorsal view of internal mold, showing septa.
Devonian (Schoharie grit), Schoharie, N. Y. Cat. No. S 1735. x 1.

Pentamerella fultonensis Branson

- 14-16.—Ventral, dorsal, and lateral views of exterior.
Devonian (Callaway ls.), Auxvasse church, Callaway Co., Missouri. Cat. No. S 1724. x 1.

Pentamerella cf. *pavilionensis* (Hall)

- 19.—Dorsal interior, showing important lamellæ.
Devonian, Alpine, Mich. Cat. No. S 1736. x 1.

Clorinda tumidula (Billings)

- 8, 12.—Dorsal and posterior views, showing characteristic exterior.
9, 10, 11, 21.—Ventral, anterior, dorsal, and lateral views of exterior.
Silurian (Gun River), Anticosti. Cat. Nos. S 1685, S 1693 (figs. 8, 12). x 1.

FIGS. *Gypidula multicostata* Dunbar

- 18.—Ventral interior, showing spondylium greatly thickened by growth of adventitious shell.
Devonian (Birdsong), Birdsong Creek, Camden Road, Tenn. Cat. No. S 1764. x 1.

Gypidula acutilobata procerula (Barrande)

- 22, 23, 27.—Lateral, ventral, and dorsal views, showing exterior.
Devonian (Ff₂), Koniepruss, Bohemia. Cat. No. S 1803. x 1.

Gypidula dudleyensis Schuchert

- 24, 28, 34, 37.—Dorsal, ventral, lateral, and posterior views, showing external form and ornamentation.
Silurian (Wenlock), Dudley, England. Cat. No. S 1789. x 1.

Gypidula coeymanensis Schuchert

- 26, 29.—Posterior and dorsal views of exterior. x 1.
31, 35.—Interior, showing spondylium, median septum, and brachial processes in place. x 1.5.
32.—Dorsal interior, showing plates. x 1.5.
40.—Both valves in conjunction. The spondylium and its relation to the dorsal plates are clear, and the nature of the septum is visible. x 1.5.
Devonian (Helderberg, Coeymans), Clarksville, Albany Co., N. Y. Cat. Nos. S 1697 (figs. 31, 35), S 1792 (figs. 26, 29), and S 1797 (figs. 32, 40).
38.—Posterior portion of ventral valve, showing spondylium and median septum.
Devonian (Coeymans), Indian Ladder, N. Y. Cat. No. S 1782. x 1.

Gypidula romingeri Hall and Clarke

- 36, 39.—Ventral and dorsal interiors, showing internal plates. Brachial processes broken from dorsal valve.
Devonian, Grand Lake, Presque Isle Co., Mich. Cat. No. S 1698. x 1.5.

Sieberella sieberi (V. Buch)

- 25, 30, 33.—Dorsal, lateral, and ventral views of two specimens, showing contour and profile of valves.
Devonian (Ff₂), Koniepruss, Bohemia. Cat. No. S 1721. x 1.

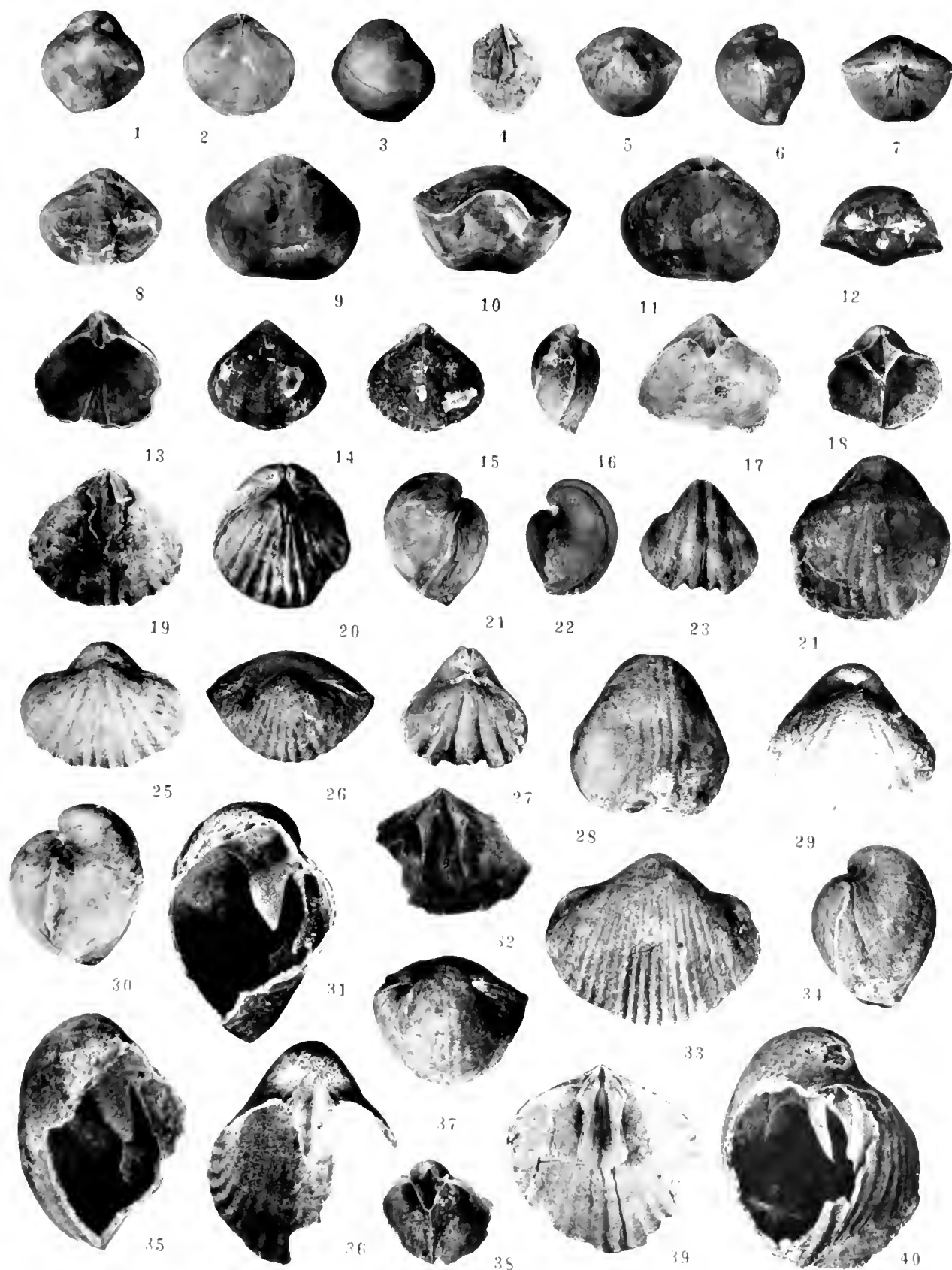


PLATE 27

FIGS. *Virgiana barrandei* (Billings)

- 1, 6, 7, 16.—Lateral, ventral, dorsal, and posterior views of a large specimen.
 Silurian (Becscie River), Becscie River, Anticosti.
 Cat. No. S 1668. x 1.

***Platyerella* aff. *manniensis* Foerste**

- 2, 3, 5, 11.—Ventral, dorsal, posterior, and lateral views of exterior.
 Silurian (Alexandrian, Sexton Creek), Belleview, Calhoun Co., Ill. Cat. No. S 1845. x 1.

***Pentamerus* cf. *oblongus* Sowerby**

- 4.—Internal septa in a specimen broken through the middle.
 8, 12, 18.—Lateral, dorsal, and ventral views of exterior.
 10.—Dorsal exterior of a young specimen.
 Silurian (Clinton), Rochester, N. Y. Cat. Nos. S 1805, S 1833 (fig. 10), and S 1851 (fig. 4). x 1.

FIGS. *Pentamerus* aff. *oblongus* Sowerby

- 17, 19.—Posterior and dorsal views of an internal mold, showing septa.
 Silurian (Niagaran), near Richmond, Ind. Cat. No. S 1808. x 0.5.

***Pentamerus* cf. *cylindricus* Hall and Whitfield**

- 9, 15.—Ventral and dorsal views of an internal mold, showing impressions of septa.
 Silurian (Niagaran), Yellow Springs, Ohio. Cat. No. S 1826. x 0.5.

***Pentameroides subrectus* (Hall and Clarke)**

- 13, 14.—Internal molds of dorsal and ventral interiors of the same specimen. Note single septum in dorsal valve.
 Silurian (Maquoketa), Jones Co., Iowa. Cat. No. S 1848. x 1.

***Holorhynchus giganteus* Kiaer**

- 20.—Dorsal view of exterior. This genus is interesting for its possession of a free spondylium.
 Silurian (zone 5b), Sandviken, Boerum, Norway.
 Cat. No. S 2135. x 2.

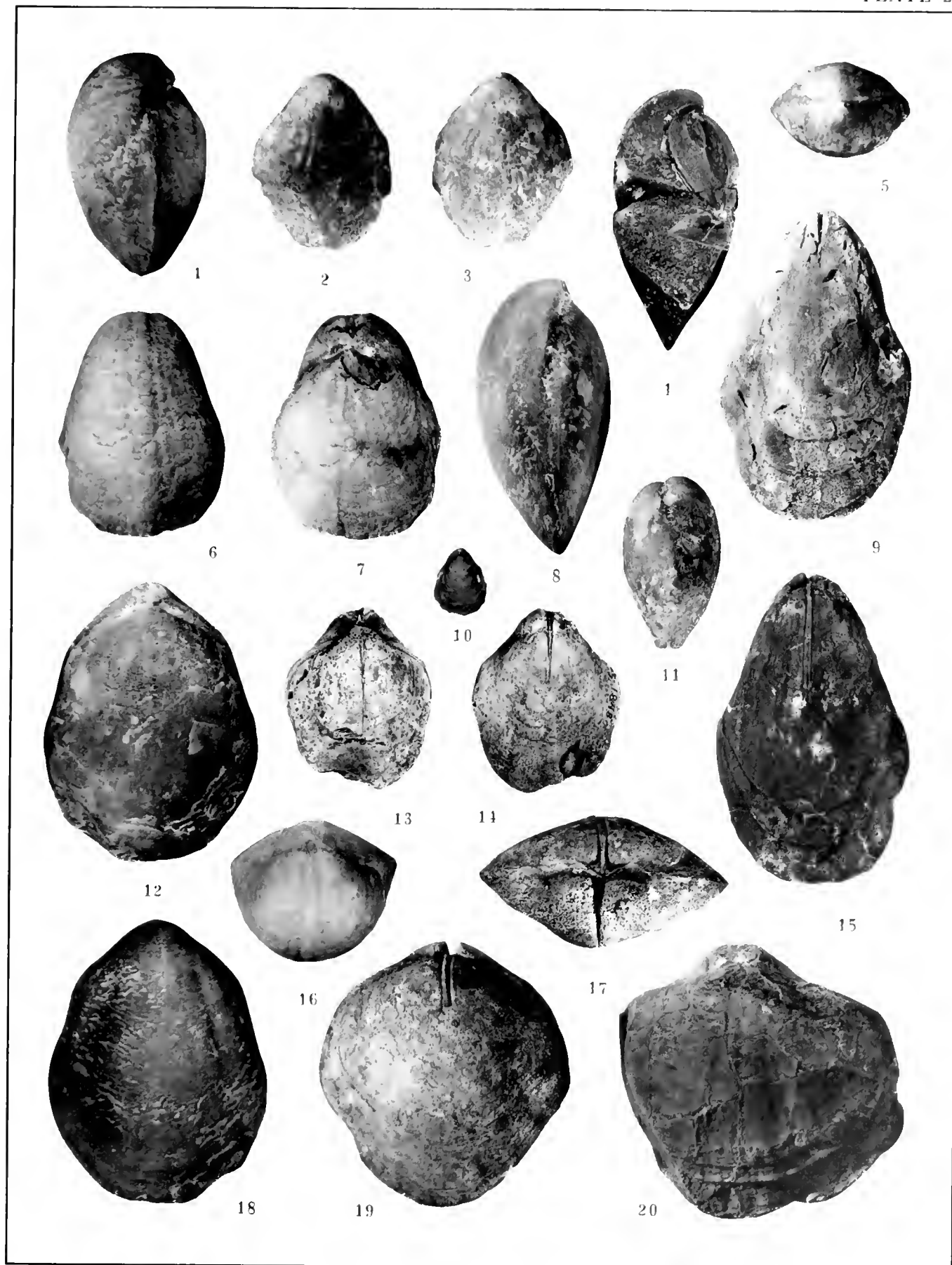


PLATE 28

FIGS. *Conchidium biloculare* Linnæus

- 1, 5, 6.—Dorsal, ventral, and lateral exteriors of a small individual.
 3.—Posterior view.
 8, 11, 12, 18.—Dorsal, ventral, lateral, and posterior views of a large specimen. Posterior view shows a remnant of the deltidium in place. Ventral view shows a long crack, marking position of median septum.
 9.—Dorsal view, showing nearly complete deltidium in place.
 Silurian (Gotlandian), Gotland, Sweden. Cat. No. S 1859. x 1.
 2.—Internal mold seen from dorsal side.
 23.—Specimen broken in plane of median septum. Long brachial process visible on the right.
 Silurian (Gotlandian), Hejde, Gotland, Sweden. Cat. No. S 1867. x 1.
 4.—Small individual in dorsal view, to show uncovered delthyrium.
 26.—Apical portion of dorsal valve with internal plates.
 Silurian, Klintehamn, Gotland, Sweden. Cat. No. S 1872. x 1.
 10.—Interior of apical portion of dorsal valve.
 20.—Spondylium of ventral valve.
 Silurian, Gotland, Sweden. Cat. No. 7839 Y. P. M. x 1.5.

Conchidium tenuistriatum Walmstedt

- 17.—Exterior of large specimen, in dorsal view.
 Silurian (Gotlandian), Gotland, Sweden. Cat. No. S 1860. x 0.5.

Lissocœlina pergibbosa (Hall and Whitfield)

- 7, 14.—Dorsal and lateral views of an internal mold, the former showing dorsal plates and the latter the unusual gibbosity.
 Silurian (Niagaran), Cedarville, Ohio. Cat. No. S 1834. x 1.

Lissocœlina ? *maquoketa* (Hall and Clarke)

- 13, 15, 16.—Ventral, dorsal, and posterior views of this gibbous pentamerid, showing internal septa. This form must be excluded from *Harpidium* because of the short median septum.
 Silurian (Niagaran), Maquoketa, Iowa. Cat. No. S 1840.

FIGS. *Lissocœlina* ? *maquoketa* (Hall and Clarke)—Cont.

- 21.—Lateral view of an unusually gibbous form.
 Silurian (Niagaran), Maquoketa, Iowa. Cat. No. S 1836.

Pentameroides subrectus (Hall and Clarke)

- 19.—Posterior view of an internal mold, showing septa. Note single septum in dorsal valve.
 Silurian (Clinton), Stony Creek, Ontario. Cat. No. S 1842. x 1.

Pentameroides, n. sp.

- 22.—View of dorsal exterior, showing single median septum.
 Silurian ("Stricklandia-Pentamerus" zone of the Clemville), Black Point, New Brunswick. Cat. No. S 1841. x 1.

Brooksina alaskensis Kirk

- 24.—Internal septa of a specimen broken through the middle.
 Silurian, S. E. shore Kosciusko Island, Davidson Inlet, S. E. Alaska. Cat. No. S 2223. x 1.

Stricklandia gaspéensis Billings

- 25.—Posterior of dorsal valve, showing brachial processes. This structure is more nearly rhynchonelloid than pentameroid. Davidson figured the brachial process affixed to the extremities of the lateral plates bounding the notothyrium.
 Silurian (La Vieille), La Vieille Cove, E. of Gascons, Quebec. Cat. No. S 1899. x 2.
 27.—Posterior of ventral valve, showing cardinal area and fractured spondylium.
 Silurian (Clinton), S. W. corner of Barachois at Port Daniel, Quebec. Cat. No. S 1887. x 1.

Stricklandia lirata (Sowerby)

- 28.—Dorsal exterior.
 Silurian, Gotland, Sweden. Cat. No. S 1883. x 1.

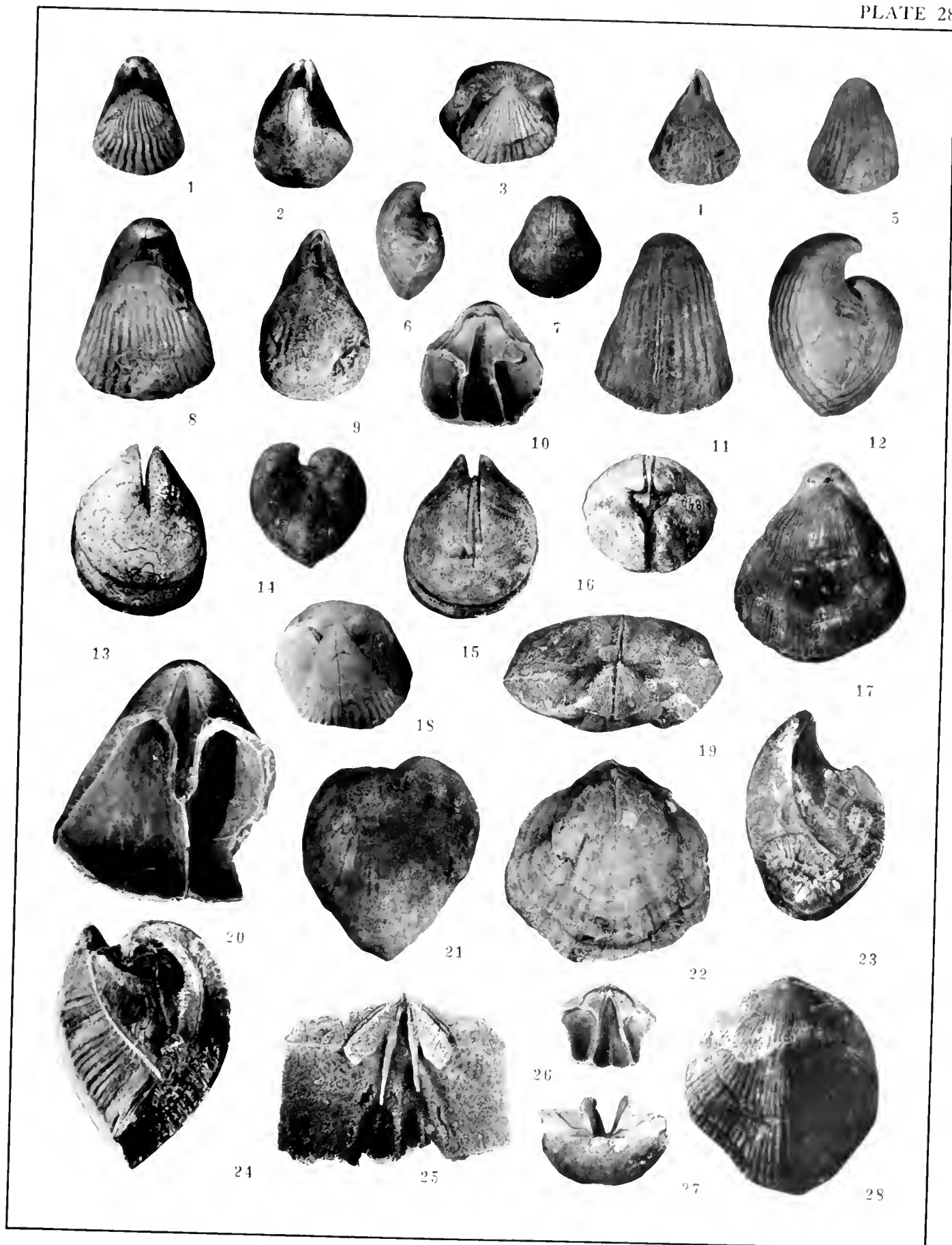


PLATE 29

FIGS. **Pionodema cf. conradi** (N. H. Winchell)

- 1.—Thin section, showing endopunctæ. It is to this type of internal shell perforation that we restrict the term endopunctæ. The section figured is a portion of the shell shown on pl. 23, fig. 9.

Ordovician (Black River), St. Paul, Minn. Cat. No. S 1367. x ca. 12.

Aulacophoria keyserlingiana (De Koninck)

- 2, 5, 10.—Ventral, dorsal, and lateral views of complete individual. Anterior like that of *Schizophoria*, but prominent fold and sulcus a divergence toward *Enteleles*.

Carboniferous, Welton, England. Cat. No. S 1924. x 1.

Hesperorthis laurentina (Billings)

- 3.—Thin section, showing deltidium in place. Cf. fig. 8. Silurian, Anticosti. Cat. No. S 2221. x 4.

Conchidium biloculare Linnæus

- 4.—Cross section of shell, showing deltidium in place. In an anterior direction from the position of this section (which is near the beaks) the deltidium becomes a flatly concave plate. In this figure the sides of the deltidium have been broken from the walls of the delthyrial cavity. In *Conchidium* the deltidium was evidently a pedicle sheath open at the posterior. A similar structure appears in *Harpidium*. See t. fig. 25.

Silurian (Gotlandian), Klintehamn, Gotland, Sweden. Cat. No. S 1872. x 3.

Stricklandia davidsoni Billings

- 6.—Section showing duplex spondylium and cardinalia. Notice also lateral elevated plates on cardinal region of dorsal valve.

Silurian (Jupiter River), East Jupiter Cliff, Anticosti. Cat. No. S 1898. x 5.

Parastrophinella reversa (Billings)

- 7.—Section showing spondylium and cardinalia. Note prominent dorsal plates and folded or duplex character of alæ in dorsal valve.

Silurian, base of White Cliff, Cape Eagle, Anticosti. Cat. No. S 1607. x 4.5.

FIGS. **Vellamo diversa** (Shaler)

- 8.—Section showing spondylium. Note thickening in umbo-lateral chambers (cf. fig. 14). Note deltidium built against delthyrial edge and strengthened by shell deposit on sides of delthyrial cavity (T = trace of tooth showing as an irregularly oval spot). x 4.5.

- 14.—Section showing umbonal chambers completely filled by adventitious shell. Note thickened deltidium and callus spread on inside of delthyrial cavity. x 3.

Ordovician (Ellis Bay), W. side Ellis Bay, Anticosti. Cat. Nos. S 2222a (fig. 8) and S 2222b.

Liocœlia proxima (Barrande)

- 9.—Section showing spondylium and cardinalia which strongly suggest *Camerophoria* and the rhynchonellids. See t. fig. 36.

Silurian (Etage Ee₂), Kolednik, Bohemia. Cat. No. S 1696a. x 4.5.

Pentamerus aff. oblongus Sowerby

- 11.—Section showing duplex spondylium and characteristic dorsal lamellæ.

Silurian (Jupiter River), Belle River, Anticosti. Cat. No. S 1819. x ca. 4.

Billingsella lindströmi (Linnarsson)

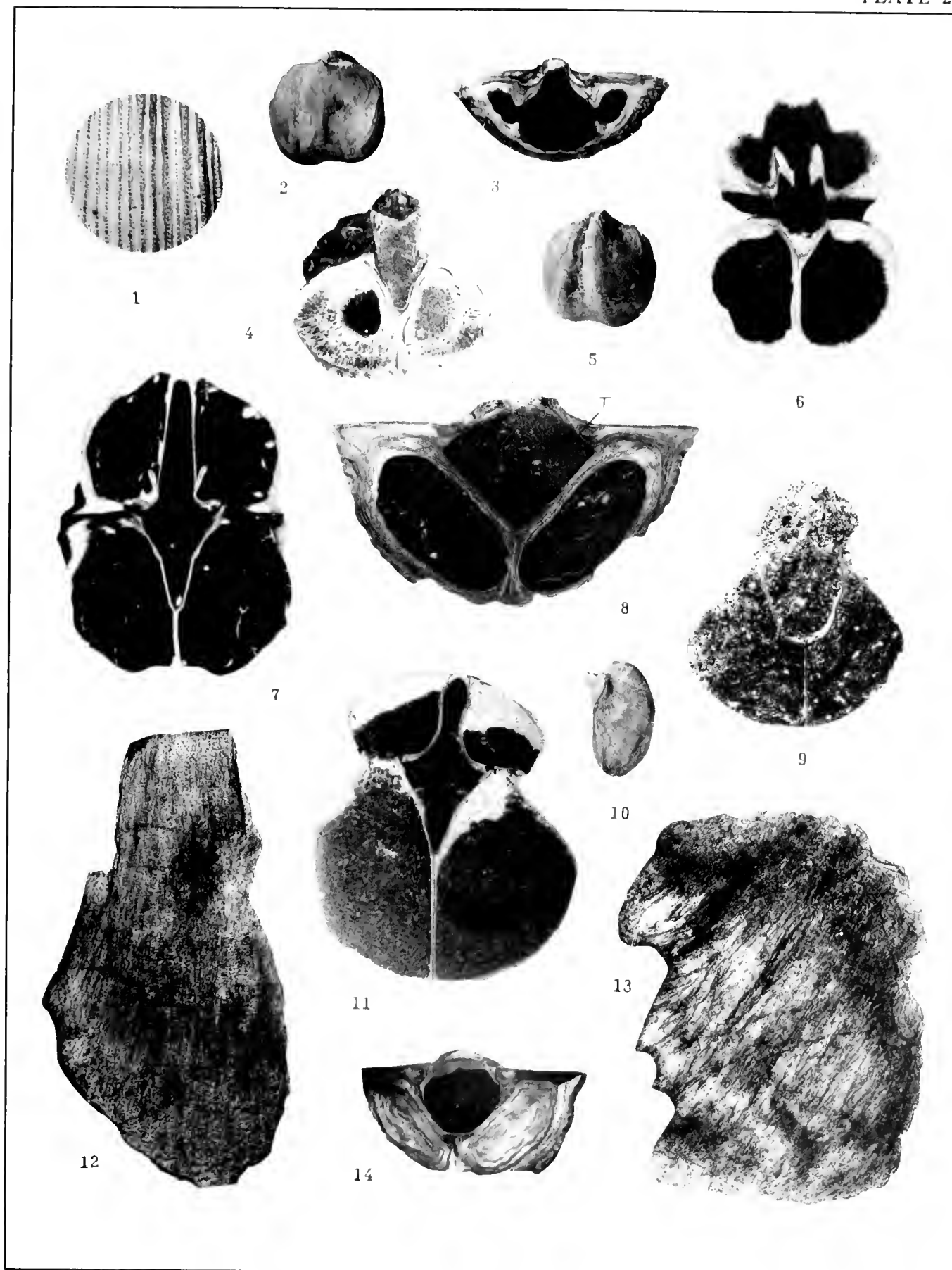
- 12.—Tangential section showing fibrous structure. Fragment of shell taken from specimen figured on pl. 1, fig. 27.

Mid. Cambrian (Paradoxides zone), Westrogothia, Lovened, Sweden. Cat. No. S 16a.

Billingsella coloradoensis (Shumard)

- 13.—This tangential section was figured by Walcott (Camb. Brach., p. 299, fig. 5) but the greater magnification used by him did not reveal the true structure. There are no punctæ in *Billingsella* and the section shows the fibers. See fig. 12.

Up. Cambrian, Morgan Creek, Burnet Co., Texas. U. S. Nat. Mus.



INDEX

The majority of the species listed in this index are not discussed in the memoir, but merely cited in the species lists to which the page number refers. Pages on which species or genera are discussed are in bold-face type. All species are listed under the specific name; in addition, species whose generic reference has been changed are listed under the genus to which they were formerly referred. Synonyms are in italics. Asterisks signify illustrations.

- abnormis* (Huenella), 159, 160*
abscissa (Panderina), **81**
actoniæ (Nicolella), **77, 78**
aculeatus (Productorthis), **82**
acuminata (Platystrophia), **65**
acutilirata (Platystrophia), **65, 66**
 prolongata (Platystrophia), **65**
acutilobus (Bilobites), **130**
acutiplicata Reed (Porambonites), **102**
acutiplicata Waagen (Enteletina), **148**
acutolobatus (Gypidula), **174**
 procerula (Gypidula), **174**
acutum (Cymbidium), **183, 184***
Adductor muscles, 6, 30, 31, 33,* 39, 40*
Adjustor muscles, 6, 30, 31, 33*
adscendens Davidson (Vellamo), **114**
adscendens Pander (Clitambonites), **26, 113**
æqualis (Hemipronites), **116**
æqualis (Orthis), **76**
æquirostris (Porambonites), **102, 104**
æquivalvis Hall (Plectorthis), **58**
 latior (Plectorthis), **58**
 pervagata (Plectorthis), **58**
æquivalvis Shaler, see *Mendacella uberis*
agilera (Nicolella), **77**
alaskensis (Brooksina), **183**
alberta (Nisusia), **45**
alsa (Rhipidomella), **133**
altaica (Rhipidomella), **134**
alternata (Heterorthis), **137**
altirostris (Rhipidomella), **133**
altissimus (Clitambonites), **114**
altus (Clitambonites), **113**
altus (Hemipronites), **116**
altus (Porambonites), **102**
alveata (Hebertella), **60**
 richmondensis (Hebertella), **60**
ambigua ("Camerella"), **168**
americana (Vellamo), **114**
amii (?) (Nisusia), **45**
amœna (Platystrophia), **65**
 longicardinalis (Platystrophia), **65**
ANASTROPHIA, **162, 164, 167, 169**
ancillans (Clorinda), **172**
andii (Enteletes), **146**
angulata (Gypidula), **174**
ANGUSTICARDINIA, **69, 84**
Angusticardiniinæ, **74, 84**
annamitica (Dinorthis), **94**
annieana (Platystrophia), **65**
anomala Schlotheim (Clinambon), **115**
 anomala Walcott (Wimanella), **50**
anthonensis (Skenidioides), **72, 73**
anticostiensis Billings (Stricklandia), **187**
anticostiensis Shaler (Plæsiomys), **94**
anticostiensis Twenhofel (Virgiana), **185**
antiquata (Swantonina), **159**
aperturata (Platystrophia), **66**
Apical plates, 6, 22
apicalis Billings (Hesperorthis), **86**
apicalis Whitfield (Polytæchia), **110**
APOMATELLA, **24, 107, 117**
appalachia (Billingsella), **49**
arachne (?) (Syntrophia), **188**
arata (Pentamerella), **176**
ARCHÆORTHIS, **21, 26, 74, 80**
arcticum (Conchidium), **181**
arcuaria (Isorthis), **150**
areola (Mystrophora), **22, 131, 132***
arethusia (?) (Syntrophia), **188**
arisaigensis (Mendacella), **127**
arkansana (Rhipidomella), **133**
armanda (Finkelburgia), **55**
armata (Clorinda), **171**
Articulation, 6, 24
assimilis (Rhipidomella), **133**
asteroidea (Nicolella), **77**
atava (Orusia), **54**
atavoides (Dinorthis), **94**
Athyris (?) *tumidula*, see *Clorinda*
Atrypa dorsata, see *Platystrophia*
 galeata, see *Gypidula*
 lens, see *Stricklandia*
 nucella, see *Lycophoria*
attenuata (Platystrophia), **65**
AULACELLA, **19, 119, 122, 136**
AULACOPHORIA, **141, 145, 147**
aurora (Eostrophomena), **85**
AUSTINELLA, **94, 99**
avelinei (Dalmanella), **120**
avita (Idiorthis), **128**

Baker, F. C., **11**
balclatchiensis (Glyptorthis), **90**
balclatchiensis (Metacamerella), **170**
Bancroft, B. B., **96, 138**
Barrande, J., **177**
barrandei Billings (Virgiana), **185, 186***
barrandei Schuchert and Cooper (Heterorthis), **138**
BARRANDELLA, **162, 163, 165, 166, 171, 173**
Barrandina, see *CLORINDA*, **172**
basalis (Parmorthis), **129**

- bassleri (Dalmanella), 120
 Bather, F. A., 13
Bathycœlia, see *PIONODEMA*
 battis (? Huenella), 160
 baueri (Porambonites), 102, **103**
 bavarica (? Archæorthis), 81
 beaumonti (Schizophoria), **143**
 beccensis (Stricklandia), 187
 Beecher, C. E., 16, 130, 131, 167
 Belanski, C. H., 175
 bella Fenton (Rhynchocamara), 189
 bella Schuchert and Cooper (Planidorsa), **101**
 bellarugosa (Glyptorthis), 90
 bellula (Pionodema), **141**
 biforata (Platystrophia), **64**
 fissicostata (Platystrophia), 66
 lynx reversata (Platystrophia), 65
 sardoa (? Platystrophia), 66
 BILLINGSSELLA, 22, 27, 28, 32, 37, 40, 41, **48**, 76
 alberta, see Nisusia
 billingsi, see Protorthis
 bivia, see Nisusia
 dice, see Deltatreta
 exporrecta, see Oligomys
 festinata, see Nisusia
 harlanensis, see Syntrophioidea
 hicksi, see Oligomys
 latourensis, see Protorthis
 orientalis, see Nisusia
 quacoensis, see Protorthis
 romingeri, see Bohemiella
 rugicostata, see Oligomys
 saffordi, see Syntrophioidea
 transversa, see Nisusia
 Billingsellidæ, 22, 27, 32, 34, 35, 37, 39, 41, 44, **48**, 107
 billingsi Hartt (Protorthis), 46
 billingsi Schuchert and Cooper (Skenidioides), 72
 billingsi Walcott (Huenella), 159
 billingsiana (Stricklandia), 187
 bilobata (Reuschella), 139
 BILOBITES, 119, **130**
 Bilobitidæ, 119, **130**
 bilobus (Bilobites), **130**
 biloculare (Conchidium), 163,* **181**, **182**
 bivia (? Nisusia), 45
 BOHEMIELLA, 50, **52**
 Booker, F. W., 163, 172, 173, 176, 181
 borealis Eichwald (Pentamerus), 178
 borealis Walcott (Wimanella), 50, **51**
 borussica (Branconia), **168**
 bouchardi (Ptychopleurella), **92**
 Brachidia, 6
 Brachiophore processes, 6, 37
 supports, 6, 37
 Brachiophores, 6, 37
 brachynota (Platystrophia), 65
 BRANCONIA, 167, **168**
 brevirostris (Anastrophia), 170
 brevis Billings (Stricklandia), 187
 brevis Pander (Hemipronites), 116
 brevis Pander (Productorthis), 82
 brevis Willard (Multicostella), 98
 breviscula (Stricklandia), 187
 bröggeri Bancroft (Dalmanella), 120
 bröggeri Lamansky (Porambonites), 102
 BROOKSINA, 163, 165, 166, 178, **183**
 bubo (Clorinda), 172
 Buckman, S. S., 14, 16, 17, 20
 burgessensis (Nisusia), 45
 burlingtonensis (Rhipidomella), 133
 Butts, C., 109
 buttsi (Orthis), 75, **86**

 caducus (Gypidula), 174
 callactis (Orthis), 7, 37, **75**, **76**
 calligramma (Orthis), 37, 76
 subplicata (Schizorammina), 88
 Calman, W. T., 12
 CAMARIUM, 6
 camerata (Platystrophia), 65
 CAMERELLA, 162, 164, 166, **167**
 bella, see Rhynchocamara
 ottawaensis, see Orthorhynchula
 varians, see Rhynchocamara
 Camerellidæ, 161, 162, 163, 164, 165, **166**, 167, 171
 campbelli (Syntrophina), **155**
 canadensis Billings (Stricklandia), 187
 canadensis Clarke (Orthostrophia), 71
 canalicula (Isorthis), 150
 canaliculata (Levenea), 124
 canalis (Resserella), 126
Capellinia, see CAPELLINIELLA
 CAPELLINIELLA, 163, 165, 166, 178, **179**
 carbonaria (Rhipidomella), 133
 Cardinal angles, 6
 area, 6
 process, 6, 34
 Cardinalia, 34, 164
 carinata (Cariniferella), **122**
 epsilon (Cariniferella), 122
 carinatus (Tropidoleptus), **152**
 CARINIFERELLA, 30, 39, 119, **122**
 carletona (Pionorthis), 95
 carleyi (Retrorsirostra), 95
 insolens (Retrorsirostra), 95
 carrickensis (Estlandia), 115
 castellana (Stricklandia), 187
 Cella, 6, 30
 celsa (Schizorammina), 87
 chama (Platystrophia), 66
 chapmani (Stricklandia), 187
 chekiangensis (Orthotichia), 144
 Chilidial plates, 6, 24
 Chilidium, 7, 23
choristites (*Enteleles*), see *Enteleles lamarki*
 chouteauensis (Schizophoria), 143
 christiania (Archæorthis), 81
 cimex (Platyorthis), 135
 circularis Pander (Hemipronites), 116
 circularis Savage (Stricklandia), 187
 circularis Sowerby (Platyorthis), 135
 circularis Winchell (Pionodema), 141
 circulus (? Mendacella), 127
 CLARKELLA, 30, 154, **156**
 Clarkellidæ, 154, **155**
 clarkensis (Rhipidomella), 133
 clarksvillensis (Platystrophia), 65
 Clements, F. E., 15, 16

- cleobis (*Rhipidomella*), 133
 clermontensis (? *Hebertella*), 60
CLINAMBRON, 107, 115
Clitambonacea, 22, 28, 43, 44, 48, 107
CLITAMBRONITES, 21, 22, 27, 29, 38, 107, 113
 americanus, see *Vellamo*
 complectens, see *Vellamo*
 diversa altissima, see *Vellamo*
 multistriata, see *Vellamo*
 planus retroflexus, see *Billingsella reflexa*
 rogersensis, see *Vellamo*
 ruedemanni, see *Vellamo*
 semiconvexus, see *Pomatotrema*
 trentonensis, see *Vellamo*
Clitambonitidæ, 17, 22, 27, 33, 35, 37, 42, 48, 110
Clitambonitinae, 107, 113
CLORINDA, 162, 163, 165, 166, 171, 178
 becsciensis, see *Stricklandia*
 fornicata, see *Barrandella*
 ventricosa, see *Barrandella*
clytie (*Heterorthis*), 40,* 137
coeymanensis (*Gypidula*), 174
 prognostica (*Gypidula*), 174
colbiensis (*Platystrophia*), 65
 mutata (*Platystrophia*), 65
colletti (*Conchidium*), 181
coloradoensis (*Billingsella*), 41, 48, 49
columbia (*Plasiomys*), 94
comis (*Gypidula*), 174
Commissure, 7, 19
complectens (*Vellamo*), 114
 albida (*Vellamo*), 114
compressus (*Pentamerus*), 178
compta ("Nisusia"), 46
concava Hortedahl (*Palæostrophomena*), 100
concava Schmidt (*Cyrtonotella*), 77
concavoconvexa (*Parmorthis*), 129
concavus Pahlen (? *Clitambonites*), 113
CONCHIDIUM, 162, 163, 164,* 165, 166, 172, 178, 181
concinna (? *Levenca*), 123
conradi (*Pionodema*), 141
contractus (*Entelestes*), 146
Convexity, 7, 19, 165
convexus (*Clitambonites*), 113
cooperi (*Parentelestes*), 147
cora (*Schizophoria*), 143
cornuta (*Gypidula*), 174
 parva (*Gypidula*), 174
corpulenta (*Dalmanella*), 120
corrugatus (*Pentamerus*), 178
corryvillensis (*Platystrophia*), 65
Costæ, 7
costalis (*Hesperorthis*), 86
costata (*Platystrophia*), 66
costata (*Productorthis*), 82
Costellæ, 7
craigensis (*Skenidioides*), 72
crassa (*Platystrophia*), 66
crassicosta (*Orthis*), 76
crassicostata (*Parmorthis*), 129
crassicostella (*Planidorsa*), 101
crassiplica (*Platymere*), 183, 184
crassiplicata (*Cyclocælia*), 64
crassoradius (*Conchidium*), 181
crispa (*Glyptorthis*), 90
crispata (*Glyptorthis*), 90
Crura, 7, 37
Crural fossettes, 7, 25
 plates, 7, 165
Cruralium, 7, 39, 166
cumberlandiæ (*Rhipidomella*), 133
cumberlandicum (*Conchidium*), 181
Cumings, E. R., 55, 67, 68, 131
cumingsi (*Platystrophia*), 65
CYCLOCÆLIA, 58, 64
Cyclocæliinæ, 56, 58, 64
CYCLOSPIRA, 6, 27
cylindricus (*Pentamerus*), 178
CYMBIDIUM, 29, 166, 178, 183
cypha (*Platystrophia*), 66
 arcta (*Platystrophia*), 66
 bellatula (*Platystrophia*), 66
 tumida (*Platystrophia*), 66
CYRTONOTELLA, 74, 77
DALMANELLA, 33,* 36, 38, 39, 119, 120, 133, 135
 bellula, see *Pionodema*
 carinata epsilon, see *Cariniferella*
 cimex, see *Platyorthis*
 circularis, see *Pionodema*
 concavoconvexa, see *Parmorthis*
 conradi, see *Pionodema*
 crispata, see *Glyptorthis*
 danbyi, see *Thiemella*
 deshayesi, see *Mystrophora*
 edgewoodensis, see *Wattsellia*
 electra, see *Archæorthis*
 lævis, see *Archæorthis*
 major, see *Archæorthis*
 elmira, see *Cariniferella*
 fairmountensis, see *Heterorthisina*
 lucia, see *Platyorthis*
 macra, see *Levenca*
 perelegans, see *Isorthis*
 planoconvexa, see *Platyorthis*
 pygmaca, see *Isorthis*
 rockhousensis, see *Isorthis*
 springfieldensis, see *Parmorthis*
 subæquata, see *Pionodema*
 gibbosa, see *Doleroides*
 perveta, see *Doleroides*
 virginia, see *Cariniferella*
 waldronensis, see *Parmorthis*
 wemplei, see *Finkelburgia*
Dalmanellacea, 22, 43, 119
Dalmanellidæ, 34, 42, 119, 125, 137
dalyana (*Rhipidomella*), 133
danbyi (? *Thiemella*), 136
dartæ (*Orthostrophia*), 71
daunus (*Archæorthis*), 81
Davidson, T., 66, 92, 103, 104
davidsoni Billings (*Stricklandia*), 187
davidsoni Verneuil (*Hesperorthis*), 86
Davies, A. Morley, 14
DAYIA, 6, 27
daytonensis (*Platystrophia*), 65
 laurelensis (*Platystrophia*), 65
daytonensis (*Glyptorthis*), 90

- decipiens (*Isorthis*), 150
 decussata (*Virgiana*), 185
 deflecta (*Valcourea*), 7, 97
 deflexa (*Anastrophia*), 170
 deformatus (*Porambonites*), 102, 103
 deformis (*Stricklandia*), 187
 Deltarium, 7
 DELTATRETA, 17, 21, 22, 23, 24, 38, 107, 108
 Deltatretidæ, 48, 107
 Delthyrial cavity, 7
 Delthyrium, 7, 21, 163
 Deltidial cover, 163
 plates, 7, 163
 Deltidium, 7, 21
 demissa (*Nicolella*), 77
 Dental plates, 7, 25, 42
 sockets, 8, 34, 35*
 dentata (*Platystrophia*), 66, 68
 Denticles, 8, 34, 35*
 Derby, O. A., 39, 145
 deshayesi (*Mystrophora*), 131
 desmopleura (? *Eoorthis*), 51
 desmopleura nympha, see nympha
 diablo (? *Eoorthis*), 51
 dice (*Deltatreta*), 108, 109
 DICTYONELLA, 102
 Diductor muscles, 8, 30, 31, 32, 33,* 40
 dieneri (*Parenteleles*), 147, 148
 Dietrich, W. O., 67
 dimera (*Bilobites*), 130
 diminutiva (*Rhipidomella*), 133
 Dinorthidæ, 35, 37, 44, 93
 DINORTHIS, 10, 18, 21, 31, 35, 36, 93, 94
 carletona, see *Pionorthis*
 carleyi insolens, see *Retrorsirostra*
 columbia, see *Plæsiomys*
 deflecta, see *Valcourea*
 iphigenia, see *Plæsiomys*
 loricula, see *Valcourea*
 meedsi, see *Plæsiomys*
 arctica, see *Plæsiomys*
 germana, see *Plæsiomys*
 platys, see *Multicostella*
 recta, see *Valcourea*
 retrorsa, see *Retrorsirostra*
 retrostriata, see *Heterorthis*
 rockymontana, see *Plæsiomys*
 subquadrata, see *Plæsiomys*
 tioga, see *Cariniferella*
 transversa, see *Plæsiomys*
 ulrichi, see *Plæsiomys*
 discus (*Rhipidomella*), 133
 disparilis (*Hesperorthis*), 86
 divergens Foerste (*Pentamerus*), 178
 divergens Hall and Clarke (*Parastrophinella*), 169
 diversa (*Vellamo*), 114
 dixonii (*Orthostrophia*), 71
 DOLEROIDES, 17, 36, 58, 63
 DOLERORTHIS, 40, 74, 88
 dolomitica (*Orthotropia*), 152
 dorsata (*Platystrophia*), 66
 dorsoplicata (*Fascicostella*), 130
 dougaldensis (*Loperia*), 47
 dubia Hall 1860 (*Pentamerella*), 176
 dubia Hall 1858 (*Perditocardina*), 83, 135
 dudleyensis (*Gypidula*), 174
 dumblei (*Enteleles*), 146
 dumonti (*Cariniferella*), 122
 edgelliana (*Idiorthis*), 128
 edgewoodensis (*Wattsella*), 125
 Eichwald, E., 103
 eifelensis (*Aulacella*), 122
 electra (*Archæorthis*), 80, 81, 109
 lævis (*Archæorthis*), 81
 major (*Archæorthis*), 81
 elegans (*Enteleles*), 146
 elegantula Butts (*Paurorthis*), 80, 109
 elegantula Dalman (*Parmorthis*), 128, 130
 elegantula McEwan (*Platystrophia*), 65
 amplisulcata (*Platystrophia*), 65
 triplicata (*Platystrophia*), 65
 elegantula Walcott (*Eostrophomena*), 85
 elkhornensis (*Platystrophia*), 65
 Elles, Gertrude, 13
 ellipsoides (*Heterorthina*), 124
 ellsworthii (*Rhipidomella*), 133
 elmira (*Cariniferella*), 122
 elongata Willard (*Multicostella*), 98
 emacerata (*Dalmanella*), 32, 120, 121
 emarginata Belanski (*Sieberella*), 175
 emarginata Hall (*Rhipidomella*), 133, 134
 emarginata Pahlen (*Vellamo*), 114
 eminens (*Orthis*), 76
 eminens (*Productorthis*), 83
Encuclodema, see *CYCLOCÆLIA*
 Endopunctæ, 10, 42
 ENTELETELLA, 145, 146, 148, 162
 ENTELETES, 19, 30, 38, 140, 146, 149, 162
 acutiplicata, see *Enteletina*
 choristites, see *lamarcki*
 dieneri, see *Parenteleles*
 ferruginea, see *Enteletina*
 globosa, see *Enteletina*
 infracarbonica, see *Aulacophoria*
 latesinuata, see *Enteletina*
 pentameroides, see *Enteletina*
 sublævis, see *Enteletina*
 uralica, see *Aulacophoria*
 ENTELETINA, 146, 148
 Enteletinæ, 31, 140, 141, 145
 ENTELETOIDES, 146, 147, 148
 Eoorthidæ, 44, 50, 74
 EOORTHIS, 27, 37, 50, 51
 bavarica, see *Archæorthis*
 christianiae, see *Archæorthis*
 daunus, see *Archæorthis*
 desmopleura nympha, see nympha
 hastingsensis, see *Protorthis*
 johannensis, see *Orusia*
 newtonensis, see *Finkelnburgia*
 putillus, see *Archæorthis*
 remnicha sulcata, see sulcata
 texana, see texana
 winfieldensis, see winfieldensis
 tullbergi, see *Archæorthis*
 wimani, see *Archæorthis*
 EOSTROPHOMENA, 85
 Epidermis, 41
 erecta (? *Nisusia*), 45

- ERIDORTHIS, 19, 74, **91**
 esthonus (Pentamerus), 178
 ESTLANDIA, 38, 38,* 107, **115**
 euryone (Archæorthis), 81
 Euseptum, 8
 excavatus (? Gonambonites), 118
 excelsus (Clitambonites), 113
 exfoliata (Plectorthis), 58
 Exopunctæ, 10, 42
 expansus (Hemipronites), 116
 exponens (Conchidium), 181
 exporrectus (Oligomys), **53, 54**
 extensa McEwan (Platystrophia), 65, 68
 extensa Pander (Panderina), 78, 82
 extensa Verneuil (Glossorthis), 78
 fairmountensis (? Heterorthina), 124
 fallax Gürich (Mystrophora), 131
 fallax Salter (Schizophorella), **62**
 fasciata (Schizoramman), 87
 FASCICOSTELLA, 125, **129**
 fascigera (? Eoorthis), 51
 fausta (Glyptorthis), 90
fernalensis (Platystrophia), see McEwanella lineolata
 ferruginea (Enteletina), 148
 festinata (Nisusia), 44
 Filæ, 8
 fillistriata (Deltatreta), **108, 109**
 filosa (Porambonites), 102
 finkelburgi (Finkelburgia), **55, 56**
 FINKELBURGIA, 10, 17, 27, 28, 38, 40, **55, 71**
 Finkelburgiidae, 44, 48, **54, 56, 58**
 fissicosta (Plectorthis), 58
 fissiplica (Schizoramman), 87
 fissistriata (Schizoramman), **87**
 flabellites (Dolerorthis), 89
 dinorthis (Dolerorthis), 89
 euorthis (Dolerorthis), 89
 fissiplicata (Dolerorthis), 89
 militaris (Dolerorthis), 89
 flabellulum (Dinorthis), 94
 carrickensis (Plæsiomys), 95
 floydensis (Schizophoria), 143
 Foerste, A. F., 88, 90, 99, 184, 185
 foerstei (Platystrophia), 65
 ampla (Platystrophia), 65
 Fold, 8
 fornicata (Barrandella), 173
 fragilis (Schizophoria), 143
 frankfurtensis (Hebertella), 60
 Frech, F., 177
 frechi Flicgel (Orthotichia), 143
 frechi Wysogorsky (Orthis), 76
 freija (Orthis), 76
 frenum (Lycophoria), 105
 Fulcral plates, 8, 34, 38, 164
 fultonensis (Pentamerella), 176
 futilis (Dalmanella), 120
 galeata (Gypidula), 172, 174
 gaspéensis (Stricklandia), **187**
 Genital markings, 8, 33
 georgiæ (? Conchidium), 181
 gervillei (Fascicostella), **130**
 gibbosa (Doleroides), **63**
 giganteus (Holorhynchus), 180
 gigas (Porambonites), 102, **103**
 Girty, G. H., 147, 148
 globata (Platystrophia), 65, **66**
 globosa Eichwald (Lycophoria), 105
 globosa Girty (? Enteletina), 148
 globosa McEwan (Platystrophia), 65
 globosa Willard (Mimella), **61**
 globosus Pander (? Hemipronites), 116
 globulosa (Gypidula), 174
 globus (Gypidula), 174
 GLOSSORTHIS, 10, 23, 28, 74, **78**
 Glyptorthina, 74, **89**
 GLYPTORTHIS, 37, 74, **89**
 sublamellosa, see Ptychopleurella
 GONAMBONITES, 17, 30, 38, 107, **118**
 inflexa, see Estlandia
 marginata aspera, see Estlandia
 magna, see Estlandia
 panderi, see Estlandia
 Gonambonitina, 107, **118**
 goodwini (Rhipidomella), 133
 Gorsky, I. I., 145, 147
 gothlandicus Lebedeff (Pentamerus), 178
 gotlandica Schuchert and Cooper (Schizoramman), **88**
 grandæva (Pomatotrema), 110
 grandis Portlock (Valcourea), 97
 grandis Tolmachew (Rhipidomella), 134
 grayiæ (Vellamo), 114
 greeniei Hall and Clarke 1895 (Camerella), 168
 greeniei Hall and Clarke 1893 (Conchidium), 181
 greenoughi (Skenidioides), 72
 GYPIDULA, 162, 165, 166, 171, **173**
 Gypidulina, 162, 163, 165, **171, 173, 178**
 Hall, H. M., 15
 Hall, J., 174
 Hall and Clarke, 18, 19, 21, 26, 27, 30, 31, 34, 35, 42,
 47, 48, 58, 59, 60, 76, 86, 87, 95, 104, 106, 113, 114,
 116, 118, 120, 121, 142, 145, 151, 161, 163, 166,
 167, 168, 169, 173, 174, 176, 178, 185, 187, 188
 halli (Skenidioides), 72, 73
 hamatus (Nicolella), 77
 HARKNESSELLA, 39, 137, **138**
 Harknessellina, 35, 137, **138**
 harlanensis (Syntrophoides), **155**
 harnagensis (Smeathenella), 139
 HARPIDIUM, 163, 165, 166, 178, **180**
 hartti (Rhipidomella), 134
 hastingensis (? Protorthis), 47
 haugi (Enteleles), 146
 HEBERTELLA, 6, 10, 19, 36, 38, 58, **59, 90, 91**
 celsa, see Schizoramman
 daytonensis, see Eridorthis
 fausta, see Eridorthis
 imperator, see Mimella
 insculpta, see Glyptorthis
 lineolata, see McEwanella
 melonica, see Mimella
 nicklesi, see Eridorthis
 rogersensis, see Eridorthis
 scovillei, see Austinella
 vulgaris, see Mimella
 helena ("Protorthis"), 47
 hemiplicata Hall 1847 (Camerella), 168
 rotunda (Camerella), 168

- hemiplicata Hall 1852 (Enteleles), 146, 147
 naia (Enteleles), 146
HEMIPRONITES, 17, 38, 107, 115
 apicalis, see *Polytæchia*
 carrickensis, see *Estlandia*
 thomsoni, see *Estlandia*
 hemipronites (Hemipronites), 116
 hera (Huenella), 159
 hermitagensis (Platystrophia), 65
 Hesperorthinae, 37, 85
HESPERORTHIS, 7, 17, 21, 22, 23, 25, 26, 37, 39, 40, 74, 76, 85
 hessensis (Rhipidomella), 133
 Heterorthidæ, 136
HETERORTHINA, 36, 119, 124
 Heterorthinae, 35, 137
HETERORTHIS, 24, 36, 39, 40,* 137
 hicksi (Oligomys), 53
 highlandensis (Wimanella), 49, 50, 51
 Hinge-line, 8
 hippolyte (Archæorthis), 81
 holdeni (Plectorthis), 58
HOLORHYNCHUS, 29, 166, 178, 180
 holtedahli (Billingsella), 48
 Homæodeltidium, 22
 Homæomorphy, 16, 57, 61, 62, 63, 89, 100, 140, 175
HORDERLEYELLA, 125, 127
 horderleyensis (Reuschella), 139
HUENELLA, 27, 28, 154, 159
 triplicata, see *Huenellina*
 Huenellidæ, 154, 159
HUENELLINA, 154, 160
 humilis Fuchs (Vellamo), 114
 humilis Pander (Clitambonites), 113
 hunnebergensis ("Protorthis"), 47
 hybrida (Rhipidomella), 133
 icetas (Huenella), 160
IDIORTHIS, 125, 128
 idonea (Rhipidomella), 133
 ignota (Dalmanella), 33,* 120, 121
 imitatrix (Rhipidomella), 134
 imperator (Mimella), 61, 62
 inca (Rhipidomella), 134
 inclyta (Heterorthis), 137
 incurvata (? Productorthis), 83, 84
 indentus (Bilobites), 130
 indianola (Eoorthis), 51
 indica (Orthotichia), 144
 inflata (Plæsiomys), 95
 inflexa (? Estlandia), 115, 118
 infracarbonica (Aulacophoria), 145
 infracarbonica (Schizophoria), 143
INGRIA, 38, 107, 112
 ingrica (Apomatella), 117
 inornata (? Cyclospira), 168
 inostrantzeffi (Hesperorthis), 86, 87
 ubjaënsis (Hesperorthis), 86
 viruana (Hesperorthis), 86
 insculpta (Glyptorthis), 89
 manitoulinensis (Glyptorthis), 90
 insigne Hall (Skenidium), 73
 insigne Kirk (Harpidium), 180
 insolita (Sieberella), 175
 Interareas, 8, 20, 163, 165, 187
 intercedens (Porambonites), 102
 intermedia Pander (? Porambonites), 104
 intermedia Pander (Productorthis), 83
 intermedia Stauffer (Rhipidomella), 133
 internascens (Anastrophia), 170
 interplicata Foerste (Dolerorthis), 88
 interplicata Hall (Anastrophia), 170
 interstriata Janischevsky (Schizophoria), 143
 interstriata Willard (Dinorthis), 94, 96
 intralineata (Pentamerella), 176
 inyoensis ("Wimanella"), 51
 iones (Taffia), 47, 85
 iowensis (Schizophoria), 143, 144
 magna (Schizophoria), 143
 iphigenia (Plæsiomys), 94, 96
 isis (Syntrophina), 156
ISORHYNCHUS, 101, 102
 Isorthinae, 140, 141, 149
ISORTHIS, 36, 149
JAMESELLA, 34, 44, 46
 jamesi (Plectorthis), 58
 jerseyensis (Rhipidomella), 133
 johannensis (Orusia), 54
 jonesi (Harknessella), 138
 juba (Huenella), 160
 juvenis (Platystrophia), 65
 kankakensis (Austinella), 99, 100
 Kayser, E., 132
KAYSERELLA, 24, 119, 132
 kayseri Kozłowski (Productorthis), 83
 kayseri Waagen (Enteleles), 146
 keisleyensis (Ptychopleurella), 92
 keyserlingianus (Aulacophoria), 145
 King, R. E., 147, 149
 King, W., 66, 83
 Kirk, E., 183
 knappi (Rhipidium), 180
 knotti (Gypidula), 174
 Kolarova, F. N., 158
 Kozłowski, R., 10, 28, 41, 49, 80, 83, 84, 104, 106, 112, 132, 150, 161, 163, 164, 173
 kozłowskii (Orthotichia), 144
 kuckersensis (Porambonites), 102
 kuckersiana (Orthis), 76
 kuthani (Jamesella), 46
KUTORGINA, 34
 lævis Sowerby (Pentamerus), 177
 lævis Walcott ("Protorthis"), 47
 lævissimus (Enteleles), 146
 læviusculus (Gypidula), 174
 Lahusen, I., 106
 Lamansky, W., 78
 lamarcki (Enteleles), 146, 147
 lamellosa (Ptychopleurella), 92
 lapworthi (Ptychopleurella), 92
 laqueatum (Conchidium), 181
LAQUEUS, 32
 lata Lamansky (Panderina), 82
 lata Pander (Productorthis), 83
 latasulcata (Hebertella), 60

- Lateral areas, 8
 plates, 9
lateralis (Syntrophia), 158
latesinuatus (Enteletina), 148
laticaudatus (Porambonites), 102
laticosta (Platystrophia), 66
latiplicata (Parastrophinella), 169
latissima (Paurorthis), 79
latissimus (Hemipronites), 116
latourensis (Protorthis), 47
latus Kirk (Harpidium), 180
latus Pander (Clitambonites), 113
latus Pander (Gonambonites), 118
latus Pander (Hemipronites), 116
laurentina (Hesperorthis), 86, 87
legoensis ("Conchidium"), 183
lehuequetiana (Rhipidomella), 133
 Leidhold, C., 165, 175, 176
lens (Stricklandia), 187
lenticularis Foerste (? Mendacella), 127
lenticularis Vanuxem (Levenea), 123
lenticularis Wahlenberg (Orusia), 54, 55, 68
 atrypoides (Orusia), 54
 lyncioides (Orusia), 54
leonardensis (Enteletes), 146
leonardensis (Rhipidomella), 133
leonensis (? Thiemella), 136
lepida (Kayserella), 132
lesleyi (Huenella), 160
leucosia (Rhipidomella), 133
 LEVENEAE, 36, 39, 40, 119, 123
lewisii (Skenidioides), 72
 Likharev, B., 162
lima (Porambonites), 102
linda (Glossorthis), 78
 virgata (Glossorthis), 78
lindenense (Conchidium), 181
lindströmi (Billingsella), 41, 49
lincolata (McEwanella), 69
linguifera (Barrandella), 173
 wilkinsoni (Clorinda), 171, 172
linneyi (Orthorhynchula), 42
 LINOPORELLA, 10, 28, 38, 103, 150
Linoporellidæ, 39, 150
 LIOCÆLIA, 171, 189
liratus (Stricklandia), 187
 LISSOCÆLINA, 165, 166, 178, 179
littoni (Conchidium), 181
liumbonus (Enteletes), 146
livia (Rhipidomella), 133
logani (Rhipidomella), 133
lonensis (? Hebertella), 60
longirostris ("Camerella"), 168
 LOPERIA, 44, 47
loricula (Valcourea), 97
lotis (Gypidula), 174
loveni (Isorthis), 150
lowi (? Nisusia), 45
lucia Billings (Rhipidomella), 133
lucia Clarke (Platystrophia), 135
 LYCOPHORIA, 39
Lycophoriidæ, 44, 105
lynx (? Platystrophia), 66, 68
 moritura (Platystrophia), 65
 McEwan, Eula D., 66-69, 70
 MCEWANELLA, 31, 69
macfarlani (Schizophoria), 144, 145
macra (Levenea), 123
magna (Valcourea), 98
magnifica (Anastrophia), 170
magnicardinalis (Rhipidomella), 133
major Savage (Virgiana), 185
major Walcott (Billingsella), 49
manitouensis (Stricklandia), 187
manniense (Platymereella), 184, 185
maquoketa (? Lissocælina), 179
marginata (Estlandia), 22, 38,* 115
 asper (Estlandia), 115
 magna (Estlandia), 115
maria (Hebertella), 60
 parkensis (Hebertella), 60
 MARIONELLA, 94, 96
marmorea (Orthotichia), 144
matapedia (Ptychopleurella), 93
matura (Idiorthis), 128
maximus (Hemipronites), 116
mayvillensis (Virgiana), 185
media (? Parmorthis), 129
 Median septa, 9
meedsi (Plasiomys), 94
 arctica (Plasiomys), 94
 germana (Plasiomys), 94
meeki (Dalmanella), 36, 120, 121
melissa (Stricklandia), 187
melonica (Mimella), 33,* 61
melvillei (Rhipidomella), 134
 MENDACELLA, 39, 125, 127
meridionalis (Enteletes), 146
 MERISTA, 6, 27
merope (?? Skenidioides), 72, 73
mesoloba (? Aulacophoria), 145
mesoplatys (Rhipidomella), 134
 baylorensis (Rhipidomella), 134
 METACAMERELLA, 167, 170
 Metcalf, Z. P., 12
micellini (Rhipidomella), 133
microcamerus (Stricklandia), 187
microplocus (Enteletes), 146
 Microstructure, 41
 MIMELLA, 17, 33, 58, 61
mineolaensis (Gypidula), 174
minima Pander (Paurorthis), 79
minima Savage (Rhipidomella), 134
minnesotensis (Pionodema), 141
minor (Barrandina), 173
minuscule Barrande (Mendacella), 127
minuscule Willard (Mimella), 61
minuta Pander (Paurorthis), 79
minuta Raymond (Platystrophia), 65
mira (Capelliniella), 179
missouriensis Branson (Pentamerella), 176
missouriensis Swallow (Rhipidomella), 133
molongensis ("Pentamerella"), 176
moneta (Nicolella), 77, 78
montanensis (Clarkella), 156
monticula (Ptychopleurella), 92
morganiana (Orthotichia), 40, 144
 chihsiaensis (Orthotichia), 144

- morrowensis (Platystrophia), 65
 münsteri (Conchidium), 181
 Muir-Wood, H. M., 158
 mullochiensis (Mendacella), 127
 multicosta (Vellamo), 114
 multicostata Dunbar (Gypidula), 174
 multicostatum Hall (Rhipidium), 181
 MULTICOSTELLA, 94, 98
 multilirata (Stricklandia), 187
 multiplicata Bancroft (? Wattsella), 125
 multiplicata Hall and Clarke (Parastrophinella), 169
 multisecta Meek (Dalmanella), 120
 multistriata Hall (Schizophoria), 143
 multistriata Roemer (Sieberella), 175
 muralis (Pomatotrema), 109
 Muscle impressions, 9, 30, 39
 musculosa (Rhipidomella), 134
 Myophore, 9, 35
 MYSTROPHORA, 17, 22, 39, 119, 131
 Mystrophoridae, 39, 119, 131

 nautes (? Nisusia), 45
 navis (Dalmanella), 120
 neglecta Barrande (Isorthis), 150
 neglecta James (Plectorthis), 58
 nettelrothi Foerste (Dolerorthis), 89
 nettelrothi Hall and Clarke (Conchidium), 181
 nevadensis (Rhipidomella), 134
 newsomensis (Orthostrophia), 71
 newsomensis (Rhipidomella), 134
 newtonensis (Finkelnburgia), 55
 nicklesi (Eridorthis), 91
 NICOLELLA, 24, 74, 77
 nikschitschi (Enteletella), 148
 nisis (Schizorammina), 87
 NISUSIA, 26, 27, 34, 44
 Nisusiidae, 37, 43, 44, 50
 nitida (Platystrophia), 65
 nodocostata (Ptychopleurella), 92
 Noetling, F., 103
 NOETLINGIA, 101, 105
 nonus (Clarkella), 156
 norwoodi (Stricklandia), 187
 Notothyrial platform, 9, 34, 39
 Notothyrium, 9, 23
 Novak, O., 177
 nucella (Lycophoria), 105, 106
 nucleolata (Gypidula), 174
 nucleus (Gypidula), 174
 nundina (Syntrophina), 156
 nympa (? Eoorthis), 51
 nysius (Rhipidium), 181

 oakensis (Polytæchia), 110
 oblata (Rhipidomella), 134
 oblongus Pander (Clitambonites), 113
 oblongus Sowerby (Pentamerus), 162, 178
 subrectus, see subrectus
 obsoletum (Conchidium), 181
 obtusa (Productorthis), 82
 obtusus (Hemipronites), 116
 occasus (Rhipidomella), 134
 occidentale Hall 1852 (Conchidium), 181
 occidentalis Hall 1858 (Gypidula), 173, 174

 occidentalis Hall 1847 (Hebertella), 60
 sinuata (Hebertella), 60
 occlusa (Isorthis), 150
 ochus (? Eoorthis), 51
 oehlerti (Enteletes), 146
 Old-age characters, 42
 OLIGOMYS, 50, 53
 Onniella, see DALMANELLA
 opercularis (Platyorthis), 135
 Öpik, A., 69, 79, 100, 112, 114, 117, 118
 ops (Parastrophinella), 169
 optatus (Brooksina), 183
 orbicularis (Hemipronites), 116
 oriens ("Nisusia"), 46
 orientalis (? Nisusia), 45
 Orientation, 18
 oriskania (Schizophoria), 143
 Ornamentation, 162, 165
 Orthacea, 43, 154
 orthambonites (Orthis), 76
 Orthambonites crassicosta, see Orthis
 parvus, see Paurorthis
 rotundata, see Orthis
 trigona, see Paurorthis
 Orthidae, 33, 34, 35, 37, 39, 42, 44, 48, 73, 94, 101, 119
 Orthinae, 37, 74, 75
 ORTHIS, 18, 21, 26, 32,* 35, 37, 40,* 74, 75, 86
 actoniae, see Nicolella
 aequivalvis, see Mendacella uberis
 annamitica, see Dinorthis
 anticostiensis, see Plasiomys
 apicalis, see Hesperorthis
 areola, see Mystrophora
 attenuata, see Heterorthis
 balclatchiensis, see Glyptorthis
 basalis, see Parmorthis
 bellarugosa, see Glyptorthis
 biforata, see Platystrophia
 lynx, see Platystrophia
 bouchardi, see Ptychopleurella
 calligramma subplicata, see Schizorammina
 canalicula, see Isorthis
 canaliculata, see Levenea
 canalis, see Dalmanella
 carinata, see Cariniferella
 carleyi, see Retrorsirostra
 circularis, see Platyorthis
 concava, see Cyrtototella
 concinna, see Levenea
 corpulenta, see Dalmanella
 costalis, see Hesperorthis
 crispa, see Glyptorthis
 davidsoni, see Hesperorthis
 decipiens, see Isorthis
 dimera, see Bilobites
 disparilis, see Hesperorthis
 dorsoplicata, see Fascicostella
 edgelliana, see Idiorthis
 eifelensis, see Aulacella
 elegantula, see Parmorthis
 ellipsoides, see Heterorthis
 emacerata, see Dalmanella
 euryone, see Archæorthis

ORTHIS—*Cont.*

extensa, see Glossorthis
 fasciata, see Schizoramma
 fissiplica, see Schizoramma
 flabellites, see Dolerorthis
 dinorthis, see Dolerorthis
 euorthis, see Dolerorthis
 fissiplicata, see Dolerorthis
 militaris, see Dolerorthis
 flabellulum, see Dinorthis
 carrickensis, see Plasiomys
 frechi, see Cyrtotonotella
 freija, see Cyrtotonotella
 futilis, see Dalmanella
 gervillei, see Fascicostella
 grandis, see Valcourea
 hemipronites, see Hemipronites
 highlandensis, see Wimanella
 hippolyte, see Archæorthis
 ignota, see Dalmanella
 inclyta, see Heterorthis
 incurvata, see Productorthis
 inflata, see Plasiomys
 inostrantzefi, see Hesperorthis
 ubjaënsis, see Hesperorthis
 viruana, see Hesperorthis
 interplicata, see Dolerorthis
 kankakensis, see Austinella
 keisleyensis, see Ptychopleurella
 keyserlingiana, see Aulacophoria
 kuckersiana, see Cyrtotonotella
 lamellosa, see Ptychopleurella
 lapworthi, see Ptychopleurella
 lenticularis Vanuxem, see Levenea
 lenticularis Wahlenberg, see Orusia
 atrypoides, see Orusia
 lyncioides, see Orusia
 leonensis, see Thiemella
 lepida, see Kayserella
 lewisii, see Skenidioides
 loveni, see Isorthis
 media, see Parmorthis
 meeki, see Dalmanella
 minuscula, see Mendacella
 moneta, see Nicolella
 monticula, see Ptychopleurella
 morrowensis, see Platystrophia
 mullochensis, see Mendacella
 multisecta, see Dalmanella
 neglecta, see Isorthis
 nettelrothi, see Dolerorthis
 nisis, see Schizoramma
 oclusa, see Isorthis
 opercularis, see Platyorthis
 parvula, see Paurorthis
 pectinella sweeneyi, see Dinorthis sweeneyi
 pepina, see Billingsella
 personata, see Proschizophoria
 plicata, see Hesperorthis
 porcata, see Plasiomys
 porrecta, see Dalmanella
 punctata, see Linoporella
 punctostriata, see Linoporella
 pyramidalis, see Hesperorthis

ORTHIS—*Cont.*

quadrans, see Levenea
 radians, see Hemipronites
 redux, see Pionodema
 rigida, see Schizoramma
 rogata, see Dalmanella
 rugiplicata, see Ptychopleurella
 rustica, see Dolerorthis
 saffordi, see Multicostella
 sedgwicki, see Fascicostella
 semicircularis, see Cyrtotonotella
 semiovalis, see Dinorthis
 stracheyi, see Austinella
 striata, see Nicolella
 striatocostatus, see Plasiomys
 subcarinata Dunbar, see Levenea
 subcarinata Hall, see Levenea
 subdivisus, see Plasiomys
 subfissicosta, see Schizoramma
 sweeneyi, see Dinorthis
 tersa, see Dalmanella
 testudinaria (Dalman), see Wattsella
 testudinaria (Hall and Clarke), see Orthis rogata
 tetragonum Roemer, see Isorthis
 lata, see Isorthis
 thakil, see Dinorthis
 convexa, see Dinorthis
 trifida, see Dinorthis
 tricenaria, see Hesperorthis
 trigeri, see Isorthis
 trigonula, see Pahlenella
 turgida, see Linoporella
 uberis, see Mendacella
 unguis, see Nicolella
 vespertilio, see Harknessella
 wisbyensis, see Parmorthis
Orthisina, see CLITAMBNITES
 adscendens, see Vellamo
 complectens, see Vellamo
 concavus, see Clitambonites
 diversa, see Vellamo
 emarginata, see Vellamo
 grandæva, see Pomatotrema
 ingrica, see Apomatella
 marginata, see Estlandia
 planus altus, see Gonambonites
 pyron, see Estlandia
 schmidtii, see Clitambonites
 squamata, see Vellamo
 verneuili, see Vellamo
 wesenbergensis, see Vellamo
 volborthi, see Estlandia
 Orthoidea, **43**
 ORTHORHYNCHULA, 26, 42
 ORTHOSTROPHIA, 33, 70
 fissistriata, see Schizoramma
 Orthostrophinae, 56, 58, 70
 ORTHOTICHIA, 30, 31, 40, 140, 141, 144
 ORTHOTROPIA, 152
 ORUSIA, 38, 54, 56, 58
 Osborn, H. F., 13
 osceola (Finkelburgia), 55,* 56
 corrugata (Finkelburgia), 55
 ottawaensis (Orthorhynchula), 42

- OTUSIA, 50, **52**
 ovalis (Pentamerus), 178
 Ovarian markings, 33
 ovata (Orthis), 76
 ovata (Productorthis), 83
 oweni (Rhipidomella), 134
- PAHLENELLA, 10, 107, **117**
 PALÆOSTROPHOMENA, 94, **100**
 Paleocology, 16
 Palintrope, 9
 Pallial markings and sinuses, 9, 32, 40
 palmata (Syntrophina), 156
 Pander, C. H., 113, 117
 panderi Billings ("Camerella"), 168
 panderi Opik (Estlandia), 115
 pandariana (Orthis), 75, **86**
 PANDERINA, 74, **81**
 papyracea (Gypidula), 174
 parallela (Productorthis), 83
 parallelus (Porambonites), 102
Parastrophia, see CAMERELLA
 divergens, see Parastrophinella
 greenei, see Camerella
 hemiplicata, see Camerella
 rotunda, see Camerella
 latiplicata, see Parastrophinella
 multiplicata, see Parastrophinella
 ops, see Parastrophinella
 reversa, see Parastrophinella
 rotundiformis, see Camerella
 scofieldi, see Camerella
Parastrophina, see CAMERELLA
 PARASTROPHINELLA, 164, 166, 167, **169**
 PARENTELETES, 6, 19, 30, 145, 146, **147**
 PARMORTHIS, 22, 25, 36, 39, 125, 126, **128**
 parva Billings ("Camerella"), 168
 parva Öpik (Vellamo), 114
 parva Pander (Paurorthis), 79, 80
 Parvicostellæ, 7
 parvula Lamansky (Paurorthis), 79
 parvulus Savage (Pentamerus), 178
 patera ("Heterorthis"), 138
 pauciplicata (Platystrophia), 65
 PAURORTHIS, 10, 74, 79, **81**
 pavilionensis (Pentamerella), 176*
 pecosi (Rhipidomella), 134
 pectinella (Dinorthis), 93, 95, 96
 sweeneyi (Dinorthis), see sweeneyi
 Pedicle callist, 9, 33*
 foramen, 9
 muscles, 9, 30, 31
 pelagica (Gypidula), 174
 peloris (Rhipidomella), 134
 penelope (Rhipidomella), 134
 penniana (Rhipidomella), 134
 pennsylvanica (Rhipidomella), 134
 pentamera (? Entelestes), 146
 Pentameracca, 28, 43, **161**
 PENTAMERELLA, 165, 166, 171, **176**
 Pentameridæ, 27, 161, 162, 164, 165, **170**
 Pentamerinæ, 162, 163, 165, 166, 171, **177**
 Pentameroidea, 43, **154**
 PENTAMEROIDES, 164,* 166, 178, **179**
 pentameroides (Enteletina), 148
 PENTAMERUS, 10, 27, 162, 163, 164,* 165, 166, 177, **178**
 acutolobata, see Gypidula
 procerula, see Gypidula
 caducus, see Gypidula
 globus, see Gypidula
 knappi, see Rhipidium
 linguifera, see Barrandella
 microcamerus, see Stricklandia
 optata, see Brooksina
 pelagica, see Gypidula
 proxima, see Liocœlia
 subrectus, see Pentameroides
 ventricosus, see Porambonites
 pepina (Billingsella), 49
 peraltus (Hemipronites), 116
 PERDITOCARDINIA, 133, **135**
 perelegans (Isorthis), 36, 150
 pergibbosa (Lissocœlina), 179
 perilla (Syntrophina), 156
 perlatus (Hemipronites), 116
 perminuta (Rhipidomella), 134
 perpasta (Jamesella), 46
 macra (Jamesella), 46
 subquadrata (Jamesella), 46
 personata (Proschizophoria), 123
 pesovis (Pentamerus), 178
 PIONODEMA, 22, 23, 30, 37, 38, 139, 140, 141, 144
 globosa, see Mimella
 minuscula, see Mimella
 PIONORTHIS, 94, **95**
 PLÆSIOMYS, 10, 31, 33, 35, 94, 95, 96
 brevis, see Multicostella
 elongata, see Multicostella
 plana (Productorthis), 83
 planareas, 165
 PLANIDORSA, 24, 94, **100**
 planissimus (Productorthis), 83
 planoconvexa Butts (Taffia), **85**
 planoconvexa Hall (Platyorthis), 36, **135**
 planus (Clitambonites), 113
 planus (Gonambonites), **118**
 planus (Porambonites), 102
 retroflexus (Billingsella), 49
 PLATYMERELLA, 163, 166, 178, **184**
 PLATYORTHIS, 36, 133, **135**
 platys (Multicostella), 98
 PLATYSTROPHIA, 19, 31, 36, 55, **64**
 fernvalensis, see Mcewanella lineolata
 Platystrophiinæ, 56, 58, **64**
 playfairi (Orthis), 76
 PLECTAMBONITES, 38
 Plectambonitinæ, 112
 PLECTELLA, 38, 107, **112**
 Plectellinæ, 107, **112**
 Plectorthidæ, 34, 36, 38, 39, 44, 48, **56**
 Plectorthinæ, **57**, 58
 PLECTORTHIS, 26, 36, 38, 54, **57**, 58, 68
 crassiplicata, see Cyclocœlia
 sectistriata, see Cyclocœlia
 sordida multiplicata, see Cyclocœlia
 whitfieldi, see Austinella
 Plica, 10
 plicata Bancroft (Horderleyella), 127

- plicata Schuchert and Cooper (Rhynchocamara), 189
 plicata Sowerby (Hesperorthis), 86
 plicatella Hall (Plectorthis), 57, 58
 trentonensis (Plectorthis), 58
 plicatella Walcott (Billingsella), 49
 plummeri (Enteleles), 146
 polita ("Camerella"), 168
 poloi (Yangtzeella), 157, 158*
 polonicum (Mystrophora), 131
 polygramma (Rhipidomella), 134
 pentlandica (Rhipidomella), 134, 152
 POLYTÆCHIA, 21, 107, 110
 montanensis, see Clarkella
 POMATOTREMA, 24, 38, 107, 109
 ponderosa (Platystrophia), 66
 arnheimensis (Platystrophia), 66
 auburnensis (Platystrophia), 66
 PORAMBONITES, 7, 11, 28, 29, 39, 101, 102
 costata, see Platystrophia
 dentata, see Platystrophia
 recta, see Angusticardinia
 striata, see Angusticardinia
 Porambonitidæ, 44, 101, 103
 porcata (Plasiomys), 95
 porcias (Taffia), 47, 85
 porrecta (Dalmanella), 120
 poststriatula (Schizophoria), 143
 præceps (Clitambonites), 113
 præculta (Heterorthina), 124
 præcursor (Platystrophia), 65
 angustata (Platystrophia), 65
 latiformis (Platystrophia), 65
 prærupta (Clitambonites), 113
 precedens (Platystrophia), 65
 preoblata (Rhipidomella), 134
 preponderosa (Platystrophia), 66
 prima (Schizophoria), 143
 primordialis (? Syntrophina), 156
 proavita (Dinorthis), 94
 Productorthinæ, 74, 81
 PRODUCTORTHIS, 17, 24, 31, 35, 38, 39, 74, 82
 Productus abscissus, see Panderina
 aculeatus, see Productorthis
 brevis, see Productorthis
 costatus, see Productorthis
 eminens, see Productorthis
 extensus, see Panderina
 intermedius, see Productorthis
 latissimus, see Paurorthis
 latus, see Productorthis
 minimus, see Paurorthis
 minutus, see Paurorthis
 obtusus, see Productorthis
 ovatus, see Productorthis
 parallelus, see Productorthis
 cf. plana, see Productorthis
 planissimus, see Productorthis
 pterygoideus, see Nicolella
 quincueradiatus, see Productorthis
 tenuis, see Productorthis
 tetragona, see Panderina
 profundosulcata (Platystrophia), 66
 hopensis (Platystrophia), 66
 prominens (Hemipronites), 116
 Pronites, see CLITAMBONITES
 adscendens, see Clitambonites
 altus, see Clitambonites
 convexa, see Clitambonites
 excelsa, see Clitambonites
 humilis, see Clitambonites
 latus, see Clitambonites
 propinqua (Isorthis), 150
 PROSCHIZOPHORIA, 119, 123
 Protegulum, 10
 Protorthidæ, 37, 44, 46
 PROTORTIUS, 28, 29, 44, 46
 dougaldensis, see Loperia
 provulvaria (Schizophoria), 143
 proxima (Liocœlia), 189
 Pseudocruralium, 10, 37, 39
 pseudogaleata (? Gypidula), 166, 172, 174
 recurrens (Gypidula), 174
 Pseudointerarea, 20
 pseudolinguifera (Clorinda), 172*
 Pseudoresupination, 10, 19
 Pseudospondylium, 10, 27, 42
 pterygoideus (Nicolella), 77
 PTYCHOPLEURELLA, 23, 74, 92
 Punctæ, 10, 41, 42, 170
 punctata (Linoporella), 150, 151
 punctostriata (Linoporella), 151
 putilla (Archæorthis), 81
 pygmæa (Isorthis), 150
 pyramidalis Hall (Skenidioides), 72, 73
 pyramidalis Öpik (Vellamo), 114
 arcuata (Vellamo), 114
 pahleni (Vellamo), 114
 simplex (Vellamo), 114
 pyramidalis Twenhofel (Hesperorthis), 86
 pyriformis (Stricklandia), 187
 elongata (Stricklandia), 187
 varicosa (Stricklandia), 187
 pyron (Estlandia), 115
 quacoensis (Protorthis), 47
 quadrans (Levenea), 123
 quadriplicata (Dinorthis), 94, 96
 Quenstedt, F. A., 103
 quincueradiata (Productorthis), 83
 radians (Hemipronites), 116
 Rafinesquina (?) atava, see Orusia
 Raymond, P. E., 80, 96, 121
 raymondi (Mcewanella), 69
 recta Conrad (Valcourea), 97
 recta Pander (Angusticardinia), 69, 84
 redux (Pionodema), 141, 142
 Reed, F. R. C., 152, 170
 regularis (Platystrophia), 65
 remnicha (Eoorthis), 51, 52
 sulcata, see sulcata
 texana, see texana
 winfieldensis, see winfieldensis
 RESSERELLA, 125, 126
 resseri (Billingsella), 49
 resupinata (Dalmanella), 120

- resupinata (Schizophoria), **143, 144**
 lata (Schizophoria), **143**
 rotundata (Schizophoria), **143**
 Resupination, **10, 19**
 resupinoides (Schizophoria), **143**
 reticulatus (Porambonites), **102**
 retrorsa (Retrorsirostra), **95**
 RETRORSIROSTRA, **21, 94, 95**
 retrostriata (Heterorthis), **137**
 REUSCHELLA, **39, 137, 139**
 reuschi (Dalmanella), **120**
 reversa Billings (Parastrophinella), **169**
 reversa McCoy (Rhipidomella), **134**
 RHIPIDIUM, **165, 166, 178, 180**
 RHIPIDOMELLA, **25, 30, 31, 32, 35, 36, 39, 133**
 circulus, see Mendacella
 rhynchonelliformis, see Mendacella
 tenuilineata Foerste, see Mendacella
 tenuilineata Hall, see Thiemella
 Rhipidomellidæ, **133**
 RHYNCHOCAMARA, **189**
 Rhynchonella frenum, see Lycophoria
 globosa, see Lycophoria
 sordida, see Cyclocælia
 ? Rhynchonellacea, **189**
 rhynchonelliformis McEwan (Platystrophia), **65**
 rhynchonelliformis Shaler (Mendacella), **127**
 RHYNCHOTREMA, **84**
 ribeiro (Porambonites), **102**
 rigida (Schizorammina), **88**
 rockhousensis (Isorthis), **150**
 rockymontana (Plæsiomys), **94**
 roemeri Hall and Clarke 1893 (Gypidula), **174**
 roemeri Hall and Clarke 1893 (Sieberella) (in part), **175**
 rogata (Dalmanella), **120, 121**
 rogersensis Foerste 1909 (Eridorthis), **91**
 rogersensis Foerste 1910 (Vellamo), **114**
 romingeri Barrande (Bohemiella), **52, 53**
 romingeri Hall and Clarke (Gypidula), **174**
 rossicus (Enteletoides), **148**
 Rostration, **165**
 rotunda (Orthis), **40,* 76**
 rotundata Pander (Orthis), **76**
 rotundata Walcott (Syntrophina), **156**
 rotundiformis (Camerella), **168**
 rotundus Kirk (Harpidium), **180**
 rotundus Pander (Clitambonites), **113**
 rotundus Pander (Hemipronites), **116**
 rudis (Nicolella), **77**
 ruedemanni (Vellamo), **114**
 rugiplicata (Ptychopleurella), **92**
 rugosicostatus (Oligomys), **53**
 rustica (Dolerorthis), **89**
 osiliensis (Dolerorthis), **89**

 sadewitzensis (Orthis), **76**
 saffordi Foerste (Rhipidomella), **134**
 saffordi Hall and Clarke (Multicostella), **98**
 saffordi Walcott (Syntrophoides), **155**
 Sahni, M. R., **14**
 salme (Nicolella), **77**
 salteri (Stricklandia), **187**
 samojedicus (Pentamerus), **178**

 sandbergi (Otusia), **52**
 Sardeson, F. W., **32, 41, 121, 165**
 Savage, T. E., **183**
 Schellwien, E., **148, 149**
 SCHIZOPHORELLA, **17, 58, 62**
 arisaigensis, see Mendacella
 SCHIZOPHORIA, **6, 17, 26, 30, 31, 35, 37, 38, 40, 40,* 41, 88, 141, 143, 146,**
 mesoloba, see Aulacophoria
 Schizophoriidæ, **22, 34, 38, 139**
 Schizophoriinæ, **140**
 SCHIZORAMMA, **26, 32,* 35, 74, 87**
 schmidti Lebedeff (Pentamerus), **178**
 schmidti Noetling (Porambonites), **102, 103**
 schmidti Pahlen (Clitambonites), **113**
 schmidti Wysogorsky (Orthis), **76**
 schuchertensis (Orthotichia), **144**
 scofieldi (Camerella), **168**
 scoparium (Conchidium), **181**
 scotica (? Plectorthis), **58, 59**
 scovillei (Austinella), **99, 100**
 sectistriata (Cyclocælia), **64**
 sedaliensis (Schizophoria), **143**
 sedgwicki (Fascicostella), **130**
 semele (Rhipidomella), **134**
 semicircularis Eichwald (Cyrtonotella), **77**
 semicircularis Pander (Orthis), **76**
 semiconvexum (Pomatotrema), **110**
 semiglobata (Reuschella), **139**
 semiovalis (Dinorthis), **94**
 senecta (Schizophoria), **143, 144, 150**
 senex (Platystrophia), **65**
 Septa, **10, 29, 39, 164, 166**
 Serial sectioning, **162**
 Shaft, **10, 35**
 shallochiensis (Vellamo), **114**
 shelbyensis (Wimanella), **50**
 SIEBERELLA, **163, 165, 171, 174, 175**
 sieberi (Sieberella), **175**
 rectifrons (Sieberella), **175**
 simon (? Huenella), **160**
 simplex Foerste (Gypidula), **174**
 simplex Walcott (Wimanella), **49, 50, 51**
 sinuata (Hebertella), **59, 60**
 sinuatis (Plectorthis), **58**
 sinuatus (Porambonites), **102**
 Skenidiidæ, **39, 44, 56, 71**
 SKENIDIOIDES, **17, 38, 71, 73, 112**
 SKENIDIUM, **71, 73, 112**
 anthonense, see Skenidioides
 craigensis, see Skenidioides
 fallax, see Mystrophora
 grayiæ, see Vellamo
 greenoughi, see Skenidioides
 merope, see Skenidioides
 nodocostata, see Ptychopleurella
 polonicum, see Mystrophora
 pyramidalis, see Skenidioides
 shallochiensis, see Vellamo
 solaris, see Pionorthis
 solitaria, see Levenea
 SMEATHENELLA, **39, 137, 139**

- Socket plates, 37
 Sockets, 10, 25, 34, 35*
 sola (Pionorthis), 95
 solaris (Plasiomys), 95
 solitaria (? Levenea), 123
 solus (Zdimir), 177
 sordida (Cyclocadia), 64
 multiplicata (Cyclocadia), 64
 Sowerbyellinae, 112
 spencei (? Nisusia), 45
 spherica (Hemipronites), 116
 SPIRIFER, 22, 87
 aperturata, see Platystrophia
 chama, see Platystrophia
 liratus, see Stricklandia
 tridens, see Platystrophia
 tscheffkini, see Noctlingia
 Spirifera biforata fissicostata, see Platystrophia
 Spondylium, 10, 26, 162, 164
 Spondyloid, 11
 springfieldensis (Parmorthis), 129
 squamata (Vellamo), 114
 stracheyi (Austinella), 99
 Striae, 11
 striata Pander (Angusticardinia), 84
 striata Pander (Nicolella), 77
 striata Twenhofel (Stricklandia), 187
 striata Walcott (Billingsella), 49
 striato-costatus (Plasiomys), 95
 striatula (Schizophoria), 143, 144
 marylandica (Schizophoria), 143
 STRICKLANDIA, 161, 187
 balclatchiensis, see Metacamerella
 Stricklandidae, 161, 186
 strigosa (Platystrophia), 65
 STROPHEODONTA, 22
 STROPHOMENA, 19, 97, 165
 aurora, see Eostrophomena
 ventrocarinata, see Valcourea
 Strophomenacea, 21, 22, 48
 strophomenoides Hall (Orthostrophia), 33,* 70
 strophomenoides Raymond (Valcourea), 97
 subaequata (Pionodema), 141, 142
 gibbosa (Doleroides), 63
 perveta (Doleroides), 63
 subaequalis (Entelestes), 146
 subcarinata Dunbar (Levenea), 123
 subcarinata Hall (Levenea), 36, 123
 subcordiformis (Rhipidomella), 134
 subdivisus (Plasiomys), 95
 subelliptica (Schizophoria), 143
 subfissicosta (Schizoramma), 88
 subglobosa (Gypidula), 174
 subjugata (Hebertella), 60
 sublaevis (Enteletina), 148
 sublamellosa (Ptychopleurella), 92
 sublaticosta (Platystrophia), 65
 sublimis (Platystrophia), 66
 sublinguifer ("Pentamerella"), 176
 suborbicularis (Rhipidomella), 134
 subplicata Bancroft (Harknessella), 138
 subplicata Reed (Orthis), 76
 subquadrata Bancroft (Harknessella), 138
 subquadratus Hall (Plasiomys), 32, 32,* 94, 95, 96
 subrectus (Pentameroides), 178, 179
 subrossicus (Enteletoides), 149
 Suess, E., 103
 suessi (Parentelestes), 147, 148
 acuticosta (Parentelestes), 147, 148
 sulcata (Eoorthis), 51
 Sulcus, 11
 swallowi (Schizophoria), 143
 SWANTONIA, 44, 159
 sweeneyi (Dinorthis), 23, 94
 symmetrica (Polytæchia), 110
 SYNTROPHIA, 40, 154, 158
 campbelli, see Syntrophina
 isis, see Syntrophina
 nona, see Clarkella
 nundina, see Syntrophina
 palmata, see Syntrophina
 perilla, see Syntrophina
 rotundata, see Syntrophina
 Syntrophiacea, 43, 48, 154
 Syntrophiidae, 154, 158, 161, 167
 SYNTROPHINA, 154, 155
 SYNTROPHINELLA, 156
 SYNTROPHIOIDES, 40, 154, 155
 szajnochai (Isorthis), 149
 tacens (Glossorthis), 78
 TAFRIA, 85
 Taffinae, 74, 85
 Teeth, 11, 24
 Teichert, C., 104
 tenuicosta (Rhipidium), 181
 tenuicostata Eichwald (Platystrophia), 66
 tenuicostata Weller (Rhipidomella), 134
 tenuilineata Foerste (Mendacella), 127
 tenuilineata Hall (Thiemella), 136
 tenuilineata Savage (Rhipidomella), 134
 tenuis (Productorthis), 83
 tenuistriatum (Conchidium), 181
 tenuistriatus (? Hemipronites), 116
 Terebratula lynx, see Platystrophia
 tenuicostata, see Platystrophia
 Terebratulites æquirostris, see Porambonites
 biforatus, see Platystrophia
 teretior (Porambonites), 102, 103
 tersa (? Dalmanella), 120, 121, 133, 135
 testudinaria Hall and Clarke, see Orthis rogata
 testudinaria Dalman (Wattsella), 120, 121, 125, 126
 tetragonum Pander (Clitambonites), 113
 tetragonum Pander (Orthis), 76
 tetragonum Pander (Panderina), 82
 lata (Panderina), 82
 tetragonum Roemer (Isorthis), 150
 texana Girty (? Orthotichia), 144
 texana Walcott (Eoorthis), 51
 texana Walcott (Huenella), 159, 160*
 laeviuscula (Huenella), 159
 thakil (Dinorthis), 94
 convexa (Dinorthis), 94
 trifida (Dinorthis), 94
 THIEMELLA, 19, 133, 136
 thiami (Rhipidomella), 134
 Thomas, I., 25, 26
 Thomson, J. Allan, 14, 30, 32, 33

- thomsoni (Estlandia), 115
 tioga (Cariniferella), 122
 transversa King (Rhipidomella), 134
 transversa Pander (Orthis), 76, 84
 latestriata (Orthis), 84
 transversa Walcott (Nisusia), 45
 transversus Pander (Clitambonites), 113
 transversus Pander (Hemipronites), 116
 transversus Willard (Plæsiomys), 94, 96
 trempealeauensis (Billingsella), 49
 trentonensis McEwan (Platystrophia), 65, 68
 champlainensis (Platystrophia), 65
 perplana (Platystrophia), 65
 trentonensis Raymond (Vellamo), 114
 tricenaria (Hesperorthis), 23, 86, 87
 tridens (Platystrophia), 66
 trigeri (Isorthis), 150
 trigona (Paurorthis), 79
 trigonula (Pahlenella), 117
 Trilobation, 165
 trilobatum (Rhipidium), 181
 Triplesia lateralis, see Syntrophia
 poloi, see Yangtzeella
 primordialis, see Syntrophina
 triplesiana (Stricklandia), 187
 triplicata (Huenella), 160
 triplicatella (Plectorthis), 58
 Tropidoleptidæ, 152
 Tropidoleptus, 152
 truncatus (Porambonites), 102
 tscheffkini (Noetlingia), 105
 tschernyscheffi (Enteles), 146
 tullbergi (Archæorthis), 81
 tulliensis (Schizophoria), 143, 150
 tumidula (Clorinda), 172
 tumidus (Hemipronites), 115
 turgida (? Linoporella), 151, 152
 Twenhofel, W. H., 92, 95, 165
 typa (Marionella), 96
 typica (Syntrophinella), 156

 uberis (Mendacella), 127
 Ulrich, E. O., 27, 43, 68, 109
 ulrichi (Plæsiomys), 94, 96
 ultima (Vellamo), 114
 umbo (Orthis), 76
 unicostata (Platystrophia), 66
 crassiformis (Platystrophia), 66
 unguiforme (Conchidium), 181
 unguis Bancroft (Wattsella), 125
 unguis Sowerby (Nicolella), 77
 uniplicata Cooper (Pionodema), 141
 uniplicata McEwan (Platystrophia), 65, 68
 uticana (Platystrophia), 65
 uniplicata Nettelroth (Gypidula), 174
 uralica Gorsky (Aulacophoria), 145
 uralicum Tschernyschew (? Skenidium), 73
 utahensis Walcott 1905 (? Nisusia), 45
 utahensis Walcott 1912 (Otusia), 52

 VALCOUREA, 10, 19, 22, 23, 25,* 94, 97, 98
 vanuxemi (Rhipidomella), 134
 pulchella (Rhipidomella), 134
 variabilis (Rhipidomella), 134
 varians (Rhynchocamara), 189
 varicus (Bilobites), 130
 VELLAMO, 17, 23, 38, 107, 114
 ventricosa Hall (Barrandella), 173
 Ventricosity, 162
 ventricosus Kutorga (Porambonites), 102
 ventrocarinata (Valcourea), 97
 vermontana (? Huenella), 160
 Verneuil, E. de, 113, 117, 118
 verneuili Eichwald (Vellamo), 114
 wesenbergensis (Vellamo), 114
 verneuili Hall (Anastrophia), 169
 verneuilius (Bilobites), 130
 vespertilio (Harknessella), 138
 villenovia (Thiemella), 136
 VIRGIANA, 165, 166, 171, 178, 185
 virginia (Cariniferella), 122
 beta (Cariniferella), 122
 visbyensis (Parmorthis), 36, 129
 volborthi Billings (Camerella), 167, 168
 volborthi Pahlen (Estlandia), 115
 vulgaris (? Mimella), 61, 62
 vulvaria (Schizophoria), 143

 Waagen, W., 147, 148
 waageni (Enteles), 146
 Walcott, C. D., 22, 27, 41, 44, 45, 46, 47, 48, 49, 50, 51,
 52, 53, 54, 80
 waldronensis (Parmorthis), 129
 wallowayi (Platystrophia), 66
 WATTSSELLA, 39, 125
 Wattsellidæ, 34, 124
 wattsi (Wattsella), 121, 125
 weedi (? Huenella), 160
 weeksi (Swantonina), 159
 wemplei (Finkelburgia), 55
 wesenbergensis (Porambonites), 102
 whitfieldi (Austinella), 99
 whittakeri (Dalmanella), 120
 wichitaensis (Eoorthis), 51
 wilkinsoni (Clorinda), 171, 172
 Williams, H. S., 122, 132, 136
 WIMANELLA, 50
 wimani (Archæorthis), 81
 Winchell, N. H., 99
 Winchell and Schuchert, 23, 95, 96, 142
 winfieldensis (Eoorthis), 51
 wingi ("Protorthis"), 47
 wolfcampensis (Enteles), 146
 wordensis (Enteles), 146
 Wysogorsky, J., 69, 78, 80

 YANGTZEELLA, 30, 154, 157

 ZDİMİR, 177

